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ERRATA

On p. 29, 30, 39, for *Seriocarpus* read *Scricocarpus*.

TEMPERATURE, THIAMINE, AND GROWTH OF
PHYCOMYCES

WILLIAM J. ROBBINS AND FREDERICK KAVANAGH

Temperature has a marked effect upon the growth of *Phycomyces blakesleeanus* in media containing limiting amounts of thiamine. At the lower temperatures growth is slower but the sporangiophores attain a greater length and the final dry weight of the mycelium is materially larger. The interrelation between thiamine and temperature on the growth of *Phycomyces* may affect our ideas of the metabolism of thiamine by this organism, bears on the use of this fungus in the bioassay of thiamine, and modifies our concept of the term "optimum" temperature. The present study reports experiments on the growth of *Phycomyces* in solution cultures at various temperatures in the presence of limiting amounts of thiamine or its intermediates.

METHODS AND MATERIALS

Phycomyces blakesleeanus (-) was grown in 125-ml. Erlenmeyer flasks each containing 25 ml. of a basal medium¹ supplemented with thiamine (or mixtures of its intermediates) in amounts less than sufficient to allow maximum growth. The medium in the flasks was inoculated by adding a drop of a spore suspension in sterile distilled water. Identical cultures were incubated at various temperatures; at intervals after inoculation the dry weights of the mycelium were determined. The dry weights of small quantities of mycelium were determined by filtering into Gooch crucibles, washing thoroughly with distilled water, and drying at 100° C. When growth was sufficiently extensive to form a mat, the mat was fished out, washed in distilled water, pressed partially dry with the fingers and placed in aluminum pans for drying and weighing.

All glassware was cleaned with chromic acid cleaning mixture, thoroughly rinsed with tap and distilled water, and drained dry. The thiamine and its intermediates were obtained from Merck and Co. The asparagine was purified by treatment with Norit and crystallization from alcohol. The other chemicals were of C.P. grade.

EXPERIMENTS

Dry Weight—Time Curves at Various Temperatures. *Phycomyces* was grown at 10°, 15°, 20°, and 25°² in the basal medium with 3 g. of

¹ The basal solution contained per liter 0.5 g. $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 1.5 g. KH_2PO_4 , 50 g. dextrose, asparagine as indicated, and the following trace elements in p.p.m.: 0.005 B, 0.02 Cu, 0.1 Fe, 0.01 Mn, 0.01 Mo, 0.09 Zn, and 0.01 Ga.

² For simplicity the temperatures of incubation are given to the nearest whole degree. They were actually as follows: 10.4° ± 0.2, 15.4° ± 0.4, 20.0° ± 0.3, and 24.8° ± 0.3. All temperatures are expressed on the Centigrade scale.

asparagine per liter supplemented with 0.25, 0.5, 1.0, or 1.5 μ moles of thiamine per flask. At various intervals after inoculation the dry weights³ of triplicate cultures were determined.

The most complete series of determinations was made on those cultures supplemented with 1.0 μ mole of thiamine. For the cultures grown with this

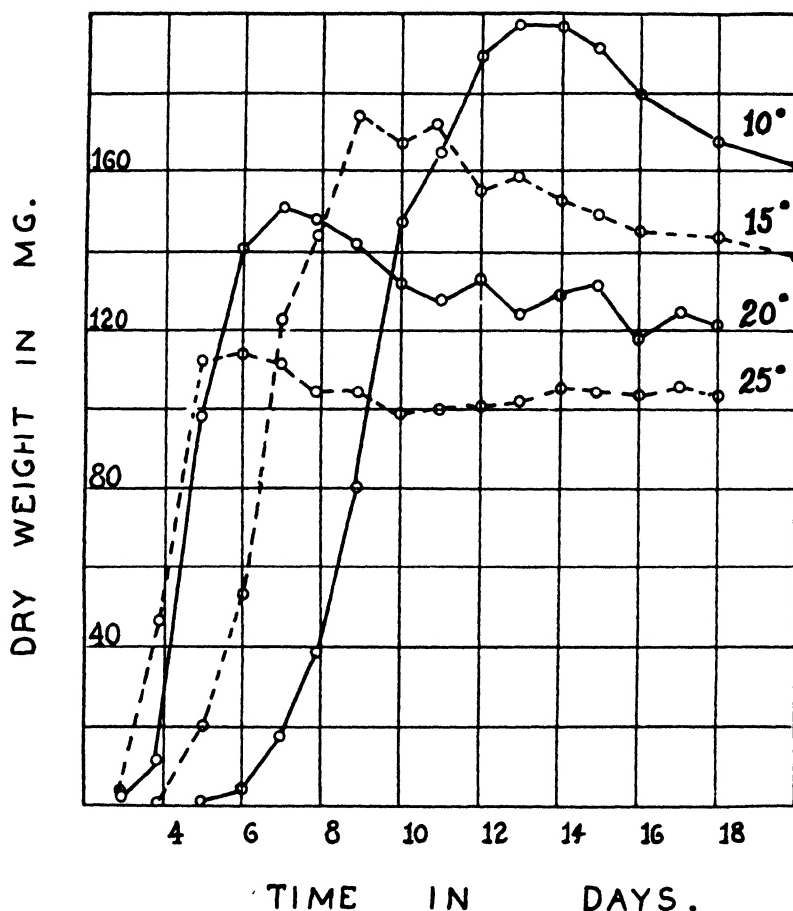


FIG. 1. Average dry weights of mycelium of *Phycomyces* produced at 10°, 15°, 20°, and 25° in a basal solution containing 1 μ mole thiamine per flask.

amount of thiamine at 10° dry weights were determined daily from the 5th to the 16th day after inoculation and on the 20th, 22nd, 24th, and 26th day. For those cultures at 15° dry weight determinations were made daily from the 4th to the 16th day and on the 18th, 20th, and 22nd day. For the cultures

³ In this experiment variations in water content in the dried mycelium were minimized by removing the mycelium from the oven and allowing it to cool for at least 30 minutes in a desiccator over calcium chloride. Weighings were made to the nearest 0.1 mg. in 30 seconds.

at 20° and 25° the determinations were made daily from the 3rd to the 18th day. The dry weight—time curves (fig. 1) at all four temperatures were of the same general shape. At each temperature the dry weight increased with time to a maximum followed by a decrease as the result of autolysis. The higher the temperature the more quickly the maximum was reached and the lower was that dry weight. At 10° with 1.0 mμ mole of thiamine the maximum dry weight was 196.8 mg. reached on the 13th day; at 15°, 167.9 mg. on the 10th day; at 20°, 152.9 mg. on the 7th day, and at 25°, 113.6 mg. on the 6th day. Almost twice as much dry matter was produced by *Phycomyces* at 10° with 1.0 mμ mole of thiamine as was formed in the same medium at 25°.

TABLE 1. Average dry weight in mg. of mycelium of *Phycomyces* grown at 10°, 15°, 20°, or 25° for the periods given in a basal solution containing 0.25, 0.5, 1.0, or 1.5 mμ moles of thiamine

Days:		5	7	10	12	13	18	20	22	28
0.25 mμ mole thiamine	10°		21.7	58.0	72.9			54.1		52.2
	15°	18.7	51.8	62.6		53.1			51.0	
	20°	47.6	51.2	41.6		43.8	51.3			
	25°	42.5	38.4	38.6		39.6	43.5			
0.5 mμ mole thiamine	10°		24.5	105.1	129.5			101.0		90.7
	15°	28.2	95.6	105.5		89.6			84.3	
	20°	85.8	86.3	71.0		68.0	67.2			
	25°	71.2	70.1	66.9		63.7	66.1			
1.0 mμ mole thiamine	10°	2.0	18.3	148.3	189.8	196.8	168.3	162.2	151.5	135.9
	15°	20.2	123.1	167.9	157.8	159.1	143.4	139.9	133.3	
	20°	99.2	152.9	132.4	133.2	124.5	122.0			
	25°	113.3	112.3	99.2	101.1	102.9	104.1			
1.5 mμ moles thiamine	10°		46.5	203.4	225.8			180.8		160.5
	15°	58.6	187.5	190.0		181.7			161.2	
	20°	179.0	186.8	186.5		167.8	161.5			
	25°	156.4	153.7	133.2		133.5	141.7			

Less frequent determinations of dry weights were made with the other quantities of thiamine. At 10° determinations were made on the 7th, 10th, 12th, 20th, and 26th day; at 15°, on the 5th, 7th, 10th, 13th, and 22nd day; at 20° and 25°, on the 5th, 7th, 10th, 13th, and 18th day. The results (table 1) with 0.25, 0.5, or 1.5 mμ moles of thiamine per flask were similar to those obtained in the cultures which contained 1.0 mμ mole of vitamin. The maximum dry weight attained at the lower temperatures was greater than that at the higher temperatures (table 2). In the cultures containing 0.25 mμ mole of thiamine the maximum weight at 10° was 171 per cent of the maximum at 25°; in those with 0.5 mμ mole it was 182 per cent; with 1.0 mμ mole 174 per cent; and with 1.5 mμ moles 155 per cent.

The higher the temperature the less efficiently was thiamine used by *Phycomyces* in the production of dry matter. This is made clear by the

figures in table 2 and also by calculating the dry matter formed per unit of thiamine at the various temperatures. For example, in the presence of 1 $\mu\mu$ mole of thiamine *Phycomyces* at 10° produced 580,000 units of dry matter for each unit of thiamine present in the medium; at 25° the units of dry matter per unit of thiamine were 340,000.

It should be emphasized that the amount of thiamine in these cultures was the factor limiting growth at all temperatures. More than sufficient sugar, asparagine, mineral salts, and other materials were present for the amount of growth obtained. This is demonstrated by the increased growth as the thiamine was increased. For example, the maximum at 10° with 0.25 $\mu\mu$ mole of thiamine was 72.9 mg.; with 0.5 $\mu\mu$ mole, 129.5 mg.; with 1.0 $\mu\mu$ mole, 196.8 mg.; with 1.5 $\mu\mu$ moles, 225.8 mg. Similar results were obtained at 15°, 20°, and 25° (table 2).

TABLE 2. Maximum dry weights in mg. obtained at the temperatures and with the quantities of thiamine given. The figures in the parentheses are the number of days of incubation to obtain the maximum dry weight.

$\mu\mu$ moles thiamine	10°	15°	20°	25°
0.25	72.9 (12)	62.6 (10)	51.3 (7)	42.5 (5)
0.5	129.5 (12)	105.5 (10)	86.3 (7)	71.2 (5)
1.0	196.8 (13)	167.9 (10)	152.9 (7)	113.3 (6)
1.5	225.8 (12)	190.0 (10)	186.8 (7)	156.4 (5)

Two grams of asparagine per liter were found to be insufficient to allow maximum growth at 10° (4) in the presence of 1 $\mu\mu$ mole of thiamine though entirely adequate when 0.2 $\mu\mu$ mole of thiamine was used.

The Influence of Excess Thiazole or Pyrimidine on the Efficiency of Thiamine at Various Temperatures. Bonner and Buchman (1) pointed out that the dry matter produced by *Phycomyces* in the presence of a limiting amount of thiamine was materially increased if an excess of the thiazole intermediate of thiamine was present. This "thiazole effect" on *Phycomyces* was confirmed by Robbins and Kavanagh (4) and by Kavanagh (3). It appeared desirable to determine the influence of temperature on the thiazole effect.

Phycomyces was grown in the basal medium containing 4 g. of asparagine per liter supplemented per culture with mixtures of the pyrimidine and thiazole⁴ intermediates of thiamine as follows:

- 0.25 $\mu\mu$ mole pyrimidine and 0.25 $\mu\mu$ mole thiazole
- 0.25 $\mu\mu$ mole pyrimidine and 10.0 $\mu\mu$ moles thiazole
- 10.0 $\mu\mu$ moles pyrimidine and 0.25 $\mu\mu$ mole thiazole

⁴ The thiazole used was 4-methyl-5- β -hydroxyethylthiazole and the pyrimidine was 2-methyl-5-bromomethyl-6-aminopyrimidine hydrobromide.

1.0 mμ mole pyrimidine and 1.0 mμ mole thiazole
 1.0 mμ mole pyrimidine and 10.0 mμ moles thiazole
 10.0 mμ moles pyrimidine and 1.0 mμ mole thiazole

Dry weights were determined on duplicate cultures at 25° after 4, 5, 6, 7, 9, and 11 days of incubation, and at 10° after 9, 11, 12, 13, 15, and 26 days. These days were selected because it was anticipated from the earlier results with thiamine that they would probably cover the maximum growth period.

In the cultures with equimolecular amounts of thiazole and pyrimidine the results were much like these obtained in the earlier experiment with thiamine. At 10° the maximum growth obtained with 1 mμ mole of thiamine was 196.8 mg. (table 2), and with 1 mμ mole of each of the two intermediates it was 192.9 mg. (table 3). At 25° the maximum growth with 1.0 mμ mole of

TABLE 3. *Dry weights in mg. of the mycelium of Phycomyces grown for the periods given in mixtures of the pyrimidine (Pyr.) and thiazole (Th.) intermediates of thiamine. Above, temperature of incubation 25°; below, temperature of incubation 10°.*

Days	0.25 mμ mole Pyr.	0.25 mμ mole Pyr.	10.0 mμ moles Pyr.	1.0 mμ mole Pyr.	1.0 mμ mole Pyr.	10.0 mμ moles Pyr.
	0.25 mμ mole Th.	10.0 mμ moles Th.	0.25 mμ mole Th.	1.0 mμ mole Th.	10.0 mμ moles Th.	1.0 mμ mole Th.
4	22.7	19.5	23.0	16.7	33.1	15.0
5	43.3	26.4	46.8	90.5	123.7	112.8
6	42.6	61.2	48.3	108.8	152.8	116.7
7	38.8	64.5	43.3	104.0	169.4	118.1
9	37.2	63.8	42.1	95.7	172.3	110.5
11	36.8	60.5	39.5	90.0	180.1	107.5
9	38.7	38.7	27.8	41.2	43.1	39.1
11	55.9	62.5	56.7	157.2	148.4	162.3
12	62.8	67.3	63.5	190.1	207.0	191.7
13	64.8	63.8	65.5	192.9	215.9	198.5
15	58.9	74.5	64.1	191.2	210.5	203.3
26	54.7	80.1	57.3	172.6	196.1	170.1

thiamine was 113.3 mg., and with 1 mμ mole of each of the two intermediates 108.8 mg. At 10° the maximum yield with 0.25 mμ mole of thiamine was 72.9 mg., and with 0.25 mμ mole of the intermediates 64.8 mg.; at 25° 0.25 mμ mole of thiamine gave 42.5 mg. as the maximum dry weight while 0.25 mμ mole of the two intermediates produced 43.3 mg. The maximum growth at 10° was 179 per cent greater than at 25° in the cultures with 1 mμ mole of each of the two intermediates, and 150 per cent greater in the cultures with 0.25 mμ mole of the intermediates.

The thiazole effect was evidenced at both temperatures but it was more pronounced at 25° than at 10°. In the cultures at 25° supplemented with 1 mμ mole of pyrimidine and 10 mμ moles of thiazole the maximum dry weight was 180.1 mg. as compared to 108.8 mg. where equimolecular amounts

of the two intermediates were used (table 3). At 10°, however, the maximum yield with 1 mμ mole of pyrimidine and 10 mμ moles of thiazole was 215.9 mg. as compared to 192.9 mg. in the solutions containing 1 mμ mole of each of the intermediates. The maximum dry weight at 25° in the solutions containing excess thiazole was 173 per cent of that in the solutions containing

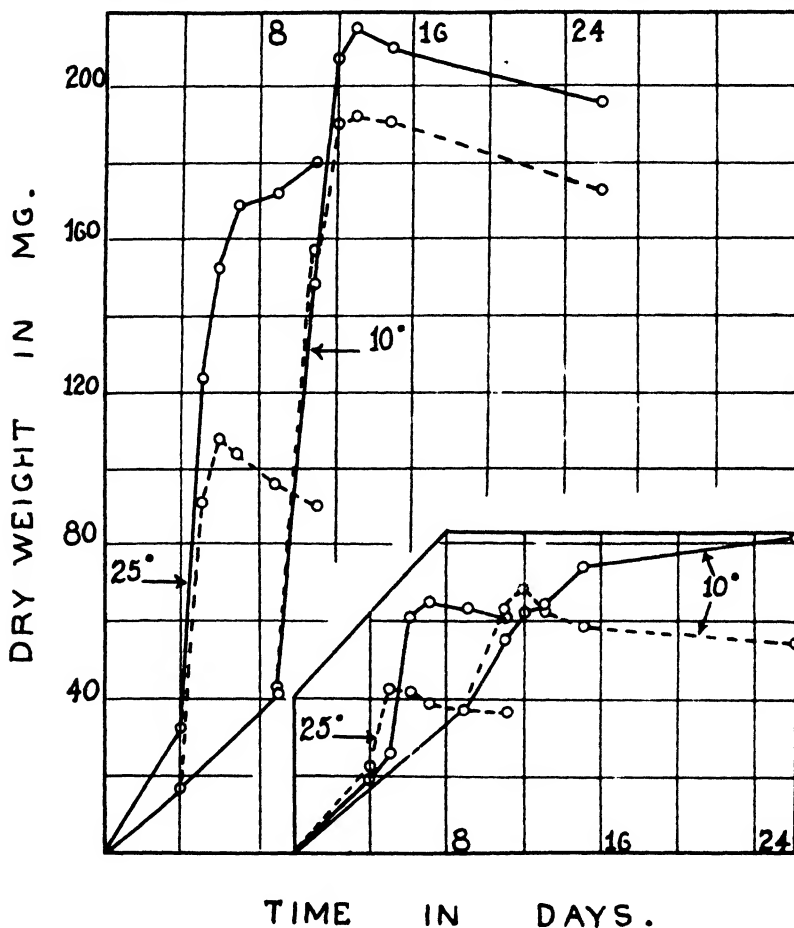


FIG. 2. Average dry weights of mycelium of *Phycomyces* produced at 10° and at 25° in solutions containing equimolecular quantities of the thiazole and pyrimidine intermediates and in solutions with excess thiazole. Above, solutions containing per flask 1 mμ mole each intermediate (broken line), or 1 mμ mole pyrimidine and 10 mμ moles thiazole (solid line). Below, solutions containing 0.25 mμ mole of each intermediate (broken line), or 0.25 mμ mole pyrimidine and 10 mμ moles thiazole (solid line).

equimolecular amounts of the two intermediates; at 10°, however, it was 112 per cent. In fact, the growth at 25° in the cultures supplemented with excess thiazole approached that at 10° in the cultures containing 1 mμ mole of each of the intermediates (fig. 2).

The same sort of results was obtained with the smaller amounts of the intermediates. The maximum dry weight at 25° in the cultures with 0.25 mμ mole of each intermediate was 38.8 mg. and with 0.25 mμ mole of pyrimidine and 10 mμ moles of thiazole it was 150 per cent greater (64.5 mg.). On the 13th day at 10° the dry weights in the solutions with equimolecular amounts of the two intermediates nearly equaled that in the solutions with excess thiazole. In the latter solutions, however, the dry weight continued to increase, reaching a value (80.1 mg.) 120 per cent greater than the maximum found in the solution with equimolecular amounts of the intermediate.

A lower temperature of incubation had much the same effect on the dry weight of *Phycomyces* under our conditions as the addition of excess thiazole to the medium. For example, the maximum dry weight at 10° with 0.25 mμ mole of the intermediates was 64.8 mg., and it was 64.5 mg. at 25° when the solution contained 0.25 mμ mole of pyrimidine and 10.0 mμ moles of thiazole. The maximum dry weight at 10° in the solutions with 1 mμ mole of the intermediates was 192.9 mg., and at 25° in the solutions containing 1 mμ mole of pyrimidine and 10 mμ moles of thiazole it was 180.1 mg. In fact, the weight (90.0 mg.) with 1 mμ mole of the intermediates at the end of 11 days growth at 25° was nearly the same as that (80.1 mg.) obtained with 0.25 mμ mole of pyrimidine and 10 mμ moles of thiazole at the end of 26 days at 10°.

Excess pyrimidine had little effect on the dry weight of *Phycomyces* as compared to that in the solutions containing equimolecular amounts of the two intermediates (table 3). There was a slight though consistently greater dry weight in those solutions containing excess pyrimidine, but whether this was a real effect or the result of some systematic error is uncertain. In any event, the action of excess pyrimidine was in no way comparable to that of excess thiazole.

DISCUSSION

Optimum Temperature for Dry Matter Production by *Phycomyces*. Burkholder and McVeigh (2) grew *Phycomyces* at 10°, 15°, 20°, and 25° with various amounts of thiamine, and concluded that the optimum temperature for the production of dry matter lies in the vicinity of 15° under the conditions of their experiments. However, they neglected the time factor and determined dry weights at one point only, namely, at the end of 10 days, a length of time insufficient for the cultures at 10° to attain their maximum dry weights. Our data show that the optimum temperature for the production of dry matter by *Phycomyces* in the presence of limiting amounts of thiamine is 10° or less. In fact, extrapolation of our data suggest that if *Phycomyces* could be grown at so low a temperature, the maximum dry weight at 2° with 1 mμ mole of thiamine per flask and 4 g. of asparagine per liter would be about 250 mg. and the thiazole effect would not appear.

The optimum temperature for the production of dry matter is influenced by the composition of the medium. We were concerned with the effects of temperature when the supply of thiamine was the limiting factor for growth. Different results would have been obtained if asparagine, dextrose, or some factor other than thiamine were limiting. For example, when 2 g. of asparagine per liter were used, we found the difference in maximum dry weights at 10° and 25° in the presence of 1 mμ mole of thiamine to be small, 126.5 mg. at the lower temperature as compared to 117.6 mg. at 25°. When 3 g. of asparagine per liter were furnished these weights were 197.2 mg. and 115.2 mg. respectively.

With the smaller amounts of thiamine Burkholder and McVeigh (2) found maximum growth at 15° C. but when 12.5, 25.0, or 2500.0 mμ moles of thiamine were supplied per flask the dry weights at the end of 10 days were nearly the same at 15°, 20°, and 25° C. They concluded that the extension of the optimum temperature range with the larger amounts of thiamine was related to the heterotrophic requirement of the fungus for thiamine. It is more probable that this apparent extension of the optimum temperature range was because asparagine or glucose limited growth in those cultures which were supplied with relatively large amounts of thiamine.

Significance for the Bioassay of Thiamine. It is clear that the temperature of incubation is important in the assay of thiamine by the growth of *Phycomyces*. A standard curve showing the relation between amount of thiamine and growth of *Phycomyces* at one temperature cannot be satisfactorily used for the bioassay of thiamine at another temperature. For example, 100 mg. of dry matter on a standard curve constructed from our data showing the relation between quantity of thiamine and maximum dry weight (5 days growth) of *Phycomyces* at 25° would represent the effect of 0.84 mμ mole of thiamine (fig. 3). If, however, the fungus were grown at 15° when a bioassay was made, a maximum dry weight of 100 mg. (10 days growth) would be produced with 0.47 mμ mole of thiamine (fig. 3). An error of comparable magnitude results if the dry weights obtained from older cultures are used instead of those which are maxima. A dry weight of 100 mg. with 10-days-old mycelium grown at 25° represented 0.98 mμ mole of thiamine as shown by our data. But 100 mg. of mycelium were produced in 20 days at 15° by 0.62 mμ mole of thiamine (fig. 3).

Relation to Concepts of the Metabolism of Thiamine. Are the results obtained with *Phycomyces* applicable to other organisms? For example, to those which require molecular thiamine and are unable to utilize the intermediates?

Bonner and Buchman (1) were of the opinion that *Phytophthora cinnamomi*, which is unable to use the intermediates of thiamine, destroys thia-

mine in the same way that *Phycomyces* does. This, they believe, occurs by the inactivation of the thiazole portion of the thiamine molecule and the releasing of functional pyrimidine. *Phycomyces* is able to couple the residual

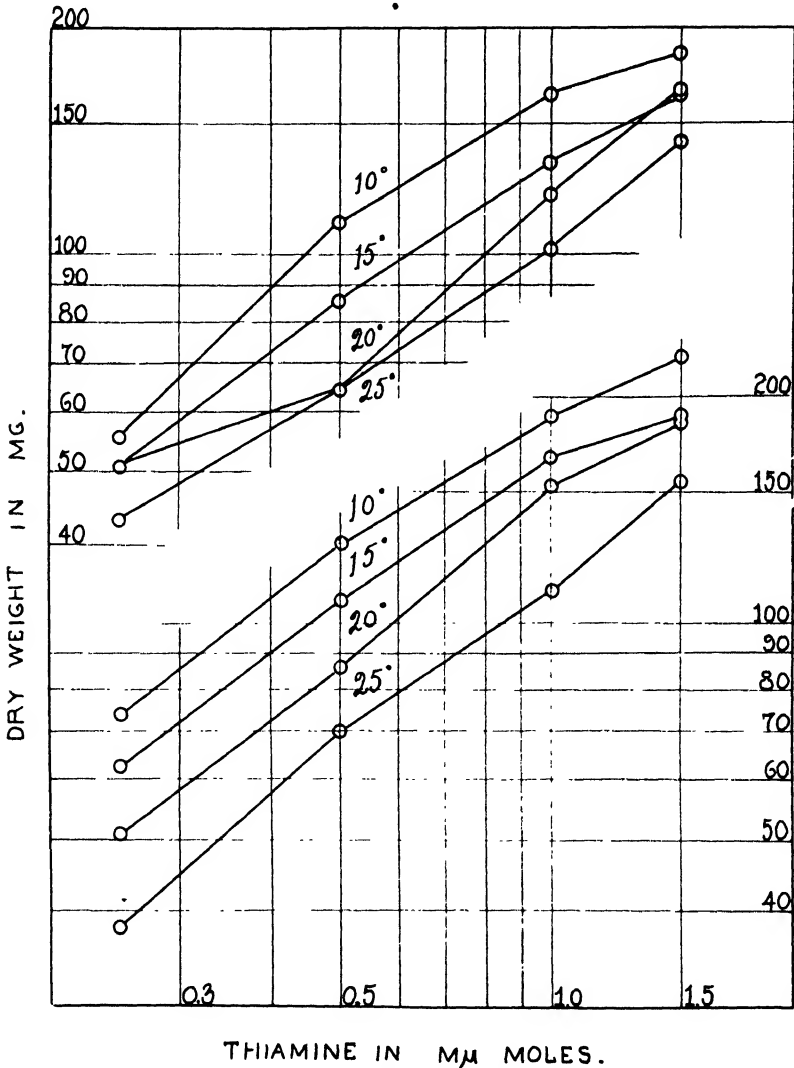


FIG. 3. Dry weights of *Phycomyces* at various temperatures plotted against quantity of thiamine on log log scales. Lower curves maximum weights at various temperatures used. Upper scale weights after 22 days at 10°; after 20 days at 15°; after 18 days at 20° and 25°.

pyrimidine with additional thiazole to form thiamine. *Phytophthora* cannot do this.

If Bonner and Buchman are correct then we should expect organisms requiring molecular thiamine also to utilize thiamine more efficiently at the lower temperatures than at higher temperatures.⁵

Kavanagh (3), however, has suggested that two enzyme systems in *Phycomyces* compete for thiamine, carboxylase and an enzyme which destroys thiazole. The latter enzyme does not exist in *Phytophthora*. If this is true, then the major effect of temperature on *Phycomyces* may be on the enzyme system which destroys thiazole rather than on the carboxylase system. Under such circumstances a marked difference might exist between the response to temperature of *Phycomyces* (and other fungi able to utilize the intermediates) in the presence of limiting amounts of thiamine, and that of organisms like *Phytophthora* which require molecular thiamine. A decision between these two viewpoints might be obtained by investigating the effect of temperature upon the growth of *Phytophthora* (or some other organism which requires molecular thiamine) in the presence of limiting amounts of this vitamin.

SUMMARY

Phycomyces was grown at 10°, 15°, 20°, and 25° in a basal solution containing limiting amounts of thiamine. The maximum dry weight increased as the temperature of incubation decreased. The efficiency with which thiamine was used by this fungus in the production of dry matter was greater at the lower than at the higher temperature. The benefit of excess thiazole was greater at 25° than at 10°. The relation of these results to the use of *Phycomyces* in bioassays and to concepts of the metabolism of thiamine is discussed.

THE NEW YORK BOTANICAL GARDEN

AND

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⁵ This conclusion would not necessarily follow if the effect of temperature on *Phycomyces* described here resulted solely from the influence of temperature upon the recombination of thiazole and pyrimidine since *Phytophthora* is incapable of this synthesis.

POLLEN ANALYSIS OF SOME BURIED SOILS, SPARTANBURG COUNTY, SOUTH CAROLINA¹

STANLEY A. CAIN

In 1936 the Soil Conservation Service² made a reconnaissance of the southern Piedmont and selected Spartanburg County, South Carolina, as a locale for intensive study of natural and accelerated erosion from the geological point of view. This is an area in which gullying has been particularly destructive because of the nature of the coincidence of land form, land use, soils, deep weathering, and climate.

The Piedmont topography of Spartanburg County is of the gently rolling type that results from the long-continued action of running water. The rounded divides slope gradually into dale heads, shallow saucer-shaped slopes, which everywhere connect with the ravines of the dendritic drainage pattern. The greater part of the area is underlaid by granites, gneisses, and schists, which under the warm, humid climate have generally weathered from 25 to 50 feet, and on the interstream divides to twice that depth below the surface. The residual soils of the area (Cecil, Lockhart, Appling, Colfax, etc.) are intimately related to the bedrock, with a badly decomposed layer, which retains the original rock structure and arrangement, intermediate between bedrock and soil.

Not only are the gullies from 20 to 25 and sometimes 50 feet deep, but a single rain may cause a gully to widen from 10 to 12 feet in places, and its cave head may recede from 10 to 15 feet within a few months. If it were not for erosion of this type, which takes place principally away from the permanent streams of the area, in dales and on the upper slopes of the gentle topography, no one would have had reason to suspect the presence of numerous, local, buried, organic soils.

Late in 1938 the author was invited to inspect certain of these organic horizons which had been discovered as a result of the gully studies around Spartanburg, and to apply the technique of pollen analysis to them, should their characteristics seem to warrant doing so. In every case these sediments, at the heads of rapidly growing gullies, rest near the upper surface of the saprolite, separated from it only by a thin sand and gravel bed, and are

¹ Contribution from the Botanical Laboratory of The University of Tennessee, N. S. No. 70.

² The following introductory paragraphs are based upon a publication of the S.C.S., "Principles of Gully Erosion in the Piedmont of South Carolina" by H. A. Ireland, C. F. S. Sharpe, and D. H. Eargle. U. S. Dept. Agr. Tech. Bull. 633. 1939. The author wishes to thank Mr. Eargle for invaluable field assistance.

buried from 5 to 20 feet or more under inorganic soils which have the typical profile structure of the residual soils of the area. After a preliminary reconnaissance and laboratory examination of some samples of these buried soils—which frequently yielded an abundance of pollen grains and spores—it was decided to study systematically some of the exposed sections with a view to seeking a possible answer to some questions with which the Division of Physiographic and Climatic Research of the Soil Conservation Service was concerned: namely, are the buried organic soils of geological age, or was their burial historic and a result of accelerated erosion following agriculture? Was the vegetation of the vicinity during the period of sedimentation similar to that prevailing today, or was it of a type associated with an entirely different climatic regimen?

METHODS

Materials for the study of several complete sections were obtained, and the present report is concerned with four apparently typical profiles from gullies here referred to as stations I (Mt. Collins, South); II (Mt. Collins, North); IV (Fingerville); and VIII (Pauline). At each station the profile, exposed in the vertical wall or head of the gully, was sampled by removal from the cleaned surface of blocks of peaty or organic soil measuring 1 × 1 × 1.5 inches. The samples were numbered from the base of the sedimentary layer upward and were taken at 3-inch intervals, i.e., with an unsampled 2-inch section between each sample. The samples were cleaned by trimming the surfaces and each sample was placed in a separate pill box where it was allowed to dry.

In the laboratory the dry, hardened samples were again cleaned by trimming, and material for the preparation of slides was shaved from the surfaces and gently powdered. The powder was passed through a brass sieve and collected in a centrifuge tube by means of a funnel. The material of a sample remained in its tube throughout the steps of preparation by the Erdtman acetolysis method (Cain 1939, p. 633). After the last centrifuging of the material all the alcohol was decanted except for about 0.5 cc., which was gently agitated in order to produce a suspension of the pollen-bearing material of the surface of the precipitate. Enough of this suspension was mounted in Sirtillac to make about 20 sq. cm. of prepared slide surface. Safranin was used as a stain, and in most preparations the pollen grains and spores were in good condition and readily studied.

The slides were examined under a binocular at a magnification of 440 diameters. A mechanical stage was employed, and strips across a slide the width of the field of vision were examined completely. For each sample enough slide area was studied to yield a minimum of 150 pollen grains of dominant tree species. All other identifiable objects were also recorded while these grains were being sought.

TABLE 1

Sample number	Woody plants													Non-woody plants										Undetermined	Undeterminable	Total					
	Dominant trees													Edaphic trees + shrubs	Flowering plant families					Spores											
	Conifers			Oak-Hickory			Mesophytes								Gramineae	Cyperaceae	Compositae	Onagraceae	Nymphaeaceae	Amaranthaceae	Asplenium	Sphagnum	Osmunda				Lycopodium	Miscellaneous			
	Pinus	Picea	Abies	Fragments	Quercus	Carya	Castanea	Tsuga	Betula	Carpinus	Liquidambar	Tilia	Nyssa																Fagus		
10	127	35	2	2				1							10	8		20	5		1			6	60	1	4	7	7	298	
9	140	3	26	5				1							7	2		1	74	1	1			1	5	3		1	7	278	
6	146	4	2	65	27	3	3	3	2	1					9	2	11	18	3	26	5	1		72	37		1	6	3	9	457
5	126	23	4	80	45	4	14		3	7					17	2	3	101	6	47	8	1		37	25				6	43	602
4	66	3	6	31	41	17	9		15	5	1				37	13	13	37	12	54	2	3		34	25		13	12	19	468	
3	114	17	1	20	12	1	15		1						13	4		41	12	8	1	2		4	5			11	24	306	
1	36	5		36	2		1								4				1					2	1		1				89
Station II Mt Collins North																															
12	32		58		73	4	41		9		1				81	11	3	17	45		2			4	7					9	397
11	58		64		82	8	7		24	2	1				5	5	6	2	7	35		5		4	2		3	4	16	340	
10	57		79		56	1	27		3	14					25	12	7	4	26	2	1	4		5	3			1	23	350	
9	66	7	3	92	46	4	21		25						17	7	26	16	5	24	2	1	3	23	17			3	5	413	
8	8		36		68	5	21		44	20	1				60	11	7	12	10	21		9		5	26	2		7	8	381	
6	94	9	110		30	3	3		9	1	1				10	8	6	20	6	15	2	9		12	14		1	1	26	390	
5	5		22		82	1	53		14	13					112	39	10	42	75		64		2	21	8			2	20	585	
3	83	3	97		33	18	12		4	6	1	1			8	14	3	1	3	23	3	1		30	2		2	3	8	360	
2	34		24		85	23	19		13	8	1				31	13	10	7	4	59	3		14	10		1	1	3	26	391	
Station IV Fingerville																															
10	20	2	43		66	46	14		4	2	2				90	5		6	5	43		11		14		10	2	5	15	405	
9	61	3	15		54	8	21		4	6					119	3	2		12	14		8		6		1		1	9	397	
8	62		77		59	24	2		5						21	4	1		3	10			32		3	3	1	11	320		
7	97		47		37	21	3		1		1	2	2		64	5	1	3	7	8		10	21	2		2		2	9	345	
6	61	9	66		53	21			4	2	4				24	4	1		5		1	1	22		4	4			16	304	
5	71	11	24	68	37	12			10	2					15	1	1		4				31			1			8	296	
4	86	3	20	64	25	17			9	1					32	1	1		4				25		1	1			8	298	
3	100	9	79		19	17			8	3	1				27	3			3	4			13		1	1	2	3	295		
2	163	17	96		33	27	4		15	4	1				7	1						1	27	2		3		1	2	310	
1	68	4	16	76	22	23	6		16		1	4	1		1	1			2	2			22	1		1	1	1	7	279	
Station VIII Pauline																															
23	11		31		107	12	10				1				12	3	3		21				2						2	215	
22	21	6	2	69	36	29	9										1		6				6						5	190	
20	5		17		123	15	44				2				3	2			4										4	219	
19	8		10		130	10	18				1	1			4		2		4				9						1	3	201
18	5		26		132	8					2	3					1		5			8	8				3	2	6	209	
17	19		39		112	17	4								1	6			1				3						3	205	
16	9		8		126	23	12				2				3	1	2		3				3						3	195	
15	15		10		95	20	51								8		1	2	4				5						3	214	
13	14		30		138	39	48								4				9				4		5				5	306	
11	4	1	7		116	7	21		6	5					43	6		21	12	4			4				1		9	269	
10			8		82	6	86		3						57	1		9	27			7	9						6	300	
9	67		69		57	9	9				2		2	1	14	2			1	2		2	5						6	248	
8	78	8	102		11	5			6						3	2							2						4	223	
7	45		118		11	15	6		2								1						3				1		1	4	207
5	104	12	2	77	19	8	2		7	1									1				7						5	245	
4	108	5	10	116	14	16	6								1	1	1	2					7				1		7	295	
3	26	1	1	15	112	7	42		1	5	1	2			6	3		3	1		1	13						3	245		
2	62		56		41	20	5		2	1	11	1	2		3	1		2	1			2	13	1	1	3		13	240		
1	71		3	54	41	31	2		3		2				3	4	3	1	5			4	20		3			7	257		

RESULTS

An analysis of the pollen is presented in table 1, in which the microfossils are classified according to a rough ecological and taxonomic scheme, and in which the number of grains or spores of each type is given for each sample from a profile. Although these tables are fairly obvious, certain items need some explanation.

The "dominant tree pollen" referred to in the introduction, and of which at least 150 were counted for each sample, are conceived as including pollen of all trees which probably entered the upper arborescent stratum of the forests represented in the sedimentation. Thus, of the tree-producing genera listed in the table, only *Alnus* and *Salix*, and the Ericaceae are excluded from this group, and *Pinus*, *Picea*, *Abies*, *Tsuga*, *Quercus*, *Carya*, *Castanea*, *Betula*, *Carpinus*, *Liquidambar*, *Tilia*, *Nyssa*, and *Fagus* make up its composition.

Some of the results of the analyses are more readily comprehended because the microfossils are classified according to the following groups:

- I. Woody plants
 - A. Dominant trees
 - 1. Coniferous genera
 - 2. Oak-hickory genera
 - 3. Mesophytic genera
 - B. Edaphic trees and shrubs
- II. Non-woody plants
 - A. Flowering-plant families
 - B. Spores
- III. Undetermined
- IV. Undeterminable

Under the heading of conifers are shown those winged pollen grains which were identified as to genus, excluding *Tsuga* which was placed with the mesophytes of the deciduous forest. Those winged pollen grains classified as "fragments" include all crushed or obscure grains not suitable for identification, and fragments of larger than half-grain size. In the summary table (table 2), where percentages are given, the fragments have been prorated among *Pinus*, *Picea*, and *Abies*. This seems a fair practice, better than to ignore them or to guess at their generic identity.

All the *Pinus* pollen grains which were observed in a suitable position were measured, as were many of the grains of *Picea* and *Abies*. The significance of these measurements is taken up in the discussion. The line labeled "undetermined" includes all pollen grains for which I have been unable to make generic or family determination. Those labeled "undeterminable" were either too distorted and obscure or were lying in an unsuitable position for determination.

In several cases no effort was made to identify the microfossil beyond the family (Ericaceae, Compositae), but for woody plants and some spores it

was usually not difficult to carry the determination to the genus. The identification of species has been attempted only for *Pinus* and *Abies*, and in each case with very interesting results.

DISCUSSION

Table 2 presents the results of the pollen analyses by genera and percentage composition, following well established practice. The percentages are computed on a basis of the dominant tree species alone. The justification for such a procedure is that it simplifies analysis and is more suggestive of the quantitative relations of the genera than when percentages are based upon all microfossils. Both of these tables are arranged according to the following ecological group totals: spruce-fir climax forest (*Picea*, *Abies*), pine subclimax forest (*Pinus* spp.), oak-hickory-chestnut climax forest (*Quercus*, *Carya*, *Castanea*), and mixed mesophytic climax forest (*Tsuga*, *Betula*, etc.). The theory is that the above grouping allows a ready interpretation of the fossil: with respect to the vegetational types and climate that prevailed at the time of the sedimentation. This theory is based upon the climatic indicator value of certain forest types at the present time, and the assumption that the past must be understood, in part at least, in terms of the present.

Although there is considerable general truth in such assumptions and interpretations, it must immediately be understood that paleo-ecological interpretations are sometimes extremely hazardous. The spruce-fir climax as a whole is an excellent indicator of certain ecological conditions of the humid microthermal climate, but in studies of a fossil flora there may be considerable representation of these genera without their having any sharp climatic indicator value. For example, species of these genera persist as postclimax relics on bog surfaces and north-facing slopes long after the spruce-fir climate as such has ceased to prevail in an area, and the dominant vegetation has developed an entirely different cast.

The genus *Pinus* provides a perfect example of the critical problem faced by the pollen analyst. Pine-dominated forests and pine-oak mixtures in eastern North America are usually considered to represent less mesophytic conditions than the contiguous climaxes. One only needs a very slight knowledge of the modern genus *Pinus* to realize that its extreme ecological variety makes broad interpretations on a basis of generic determinations alone very uncertain. There are pine species associated with nearly every tree-dominated climax in North America. Their tolerances for temperature range all the way from *P. banksiana*, which extends to the far northern continental timber line, to *P. caribaea*, which goes into the subtropics. Their tolerances for moisture vary from the species of the semi-arid piñon-juniper forests to the white pines which require mesophytic conditions. In paleo-ecological studies, as in studies of modern vegetation, one needs very much to know

TABLE 2

Ecological Groups														Group totals				
	A		B	C			D				A	B	C	D				
Sample number	Abies	Picea	Pinus	Quercus	Carya	Castanea	Tsuga	Betula	Carbinus	Liquidambar	Tilia	Nyssa	Fagus	Sprucefir climax	Pine subclimax	Oak-chestnut climax	Mixed mesophytic climax	Number of grains
Station I Mt Collins South																		
10			970	12	12		06							970	24	06		167
9	2.3		943	28			06							2.3	943	28	06	175
6	1.1	2.3	81.2	10.5	1.1	1.1	1.1	0.8	0.4					3.4	81.2	12.7	2.3	256
5	1.3	11.8	63.1	14.7	13	45	0.9	2.3						13.1	63.1	20.5	3.2	306
4	4.6	2.0	479	21.1	8.7	46	7.7	2.5	0.5					6.6	479	34.4	10.7	194
3	0.5	11.0	72.3	6.6	0.5	82		0.5						11.5	72.3	15.3	0.5	181
1		11.2	850	2.5	12									11.2	850	3.7		80
Station II Mt Collins North																		
12			413	33.5	18	188		4.1	0.4						412	54.1	4.5	218
11			496	33.3	3.2	28		9.7	0.8	0.4					496	39.3	10.9	246
10			574	23.6	0.4	114	12	5.9							574	35.4	7.1	237
9	2.3	5.3	56.0	17.4	11	8.0		9.5						7.6	56.0	26.5	9.5	264
8			216	33.4	2.8	10.3		21.6	9.8	0.5					21.6	46.5	31.9	20.3
6	7.7		742	11.5	12	12		3.4	0.4	0.4				7.7	74.2	13.9	4.2	260
5			142	43.1	0.5	27.9		7.3	6.8						14.2	71.5	14.1	190
3	2.3		68.6	12.8	7.0	4.6	15	2.3	0.4		0.4			2.5	68.6	24.4	4.6	258
2			28.0	4.1	11.1	9.1		6.2	3.8		0.5				28.0	61.3	10.5	207
Station IV Fingerville																		
10	3.0		296	33.1	23.1	70	2.0		1.0	1.0				3.0	296	63.2	4.0	199
9	2.7		554	24.3	3.6	94	1.8	2.7						2.7	554	37.3	4.5	222
8			602	25.5	10.4	0.8	2.1						0.8		60.2	36.7	2.9	231
7			682	17.5	10.0	14	0.5		0.5	0.9	0.9				68.2	28.9	2.8	211
6	7.6		53.6	23.8	9.4		1.8	0.9		1.8			0.9	7.6	53.6	33.2	5.4	222
5	17.0	7.6	49.3	15.9	5.1		4.2			0.8				24.6	49.3	21.0	5.0	235
4	14.2	2.2	60.4	11.1	7.5		4.0			0.4				16.4	60.4	18.6	4.4	225
3	6.3		72.7	8.0	7.1		3.3	1.2		0.4			0.8	6.3	72.7	15.1	5.7	238
2	13.9		52.2	12.4	10.1	1.5	5.6	1.5		0.4			2.2	13.9	52.2	24.0	9.7	266
1	13.7	2.9	52.5	9.2	9.6	2.5	7.5			0.4		1.6		16.6	52.5	21.3	9.5	240
Station VIII Pauline																		
23			244	62.2	7.0	5.8							0.6		244	75.0	0.6	172
22	2.3	6.9	47.5	20.9	16.9	5.2								9.2	47.5	43.0		172
20			10.7	59.7	7.3	21.3							1.0		10.7	88.3	1.0	206
19			10.1	73.0	5.6	10.1							0.6	0.6	10.1	88.7	1.2	178
18			17.6	75.0	4.2					1.1			1.7		17.6	79.2	2.8	176
17			30.3	58.6	8.9	2.1									30.3	69.6		191
16			9.4	70.0	12.8	6.6							1.0		9.4	89.4	1.0	180
15			13.1	49.6	10.7	26.6									13.1	86.9		191
13			17.0	53.3	11.2	18.5									17.0	83.0		259
11		1.2	6.0	69.5	4.2	12.5		3.6	3.0					1.2	6.0	86.2	6.6	167
10			4.3	44.3	3.2	46.5		1.6							4.3	94.0	1.6	185
9			63.0	26.4	4.1	4.1				0.9		0.9	0.5		63.0	34.6	2.3	216
8		7.5	81.1	5.2	2.6		2.8						0.9	7.5	81.1	7.8	3.7	212
7			82.7	5.6	7.6	3.0	1.0								82.7	16.2	1.0	197
5	1.7	10.3	72.0	8.2	3.4	0.8	3.0	0.4						12.0	72.0	12.4	3.4	232
4	7.1	3.6	74.9	5.0	5.7	2.1	1.4							10.7	74.9	12.8	1.4	279
3	0.9	0.9	18.3	52.5	3.3	19.7	0.5	2.3		0.5		0.9		1.8	18.3	75.5	4.2	213
2			58.7	20.4	9.9	2.5	1.0	0.5		5.5	0.5	1.0			58.7	32.8	8.5	201
1	2.9		58.9	18.8	15.0	1.0	1.5			1.0				2.9	58.9	35.8	2.5	207

what the species are, for the ecological tolerance of different species of the same genus may be greatly different. Nevertheless, in eastern North America, when pine pollen is considered in relation to other genera, and to changes from horizon to horizon, certain interpretations as to the significance of the pine may be made on a basis of generic determination only.

Somewhat similar problems arise in connection with the oak-hickory and oak-chestnut associations. Different oak species have tolerances ranging all the way from some which require a moist condition, tolerate a saturated soil, and never constitute a portion of the climax association (*Q. palustris*, *Q. bicolor*), to others which are climax dominants and codominants of associations of various conditions (*Q. alba*, *Q. macrocarpa*), and several species of the western montane and foothill forests.

It is usually necessary in pollen studies to group several genera under the broad heading of mixed mesophytic forest, for it is nearly always impossible to distinguish in fossil floras whether the genera were actually present as an undifferentiated mesophytic type or as a series of association segregates. As a matter of fact, this grouping of mesophytic genera usually provides as much information as is useful in pollen analysis, for the technique does not allow much refinement of interpretation in many studies.

With these preliminary cautions, we may examine table 2 for such information as it may yield. In the first place, Spartanburg is in the Piedmont in an area usually classified on a basis of modern vegetation as oak-chestnut climax association or oak-pine. The element in the fossil flora that is distinctly out of climatic harmony is that of the spruce-fir climax. This element reaches maxima of 13.1 per cent in the fifth spectrum of Station I, 7.7 per cent in the sixth spectrum of Station II, 24.6 per cent in the fifth spectrum of Station IV, and 12.0 per cent in the fifth spectrum of Station VIII. Although the representation of spruce-fir is somewhat erratic from spectrum to spectrum, especially at stations II and VIII, it is apparent that most of these fossils occur in the lower levels of the buried soils and are absent or sporadic and of low percentage in the upper half of the sediments. One is immediately led to the conclusions that the climate was somewhat cooler at the time of sedimentation than at present, and that the period of time represented by the deposits included a retrogression of spruce-fir during the upper half.

These conclusions seem warranted despite the preponderance of non-spruce-fir pollen, providing, of course, it is assumed that the spruce and fir pollen grains were not blown to the sedimentary basins from a considerable distance where a different climate prevailed. Although there are no good data on this point, there are certain facts which in this case argue against the long-distance, wind-dissemination hypothesis. The representation of spruce-fir at certain horizons is too great for them to be considered made

up of grains transported a considerable distance. Today the spruce-fir climax occurs on the high southern Appalachians about 60–100 miles northwest of the Spartanburg deposits, and the prevailing winds blow from the southeast. If the climate was cooler at the time of sedimentation than now, the spruce-fir formation would probably have occurred on more of the southern mountains than at present and also have extended its lower limits to lower altitudes. There is nothing in the spectra, however, to indicate that a spruce-fir climate prevailed at Spartanburg at the time of sedimentation. It appears more reasonable to conclude that spruce and fir grew in and locally around the small ponds where the organic deposits accumulated, and that the upland was dominated by a mixture of oak-hickory-chestnut climax and pine subclimax. Taking the views described above, it seems necessary for us to assume that the spruce-fir in the Spartanburg region played the role of postclimax relies, and that the climate even earlier—at a time not represented by these four profiles—had been more like that of spruce-fir climaxes today. One would hazard, then, that the time represented by the buried soils was probably associated with one of the waning periods of the Pleistocene, but which one is unguessed.

The above conclusions do not rest only upon the evidence of the spruce and fir pollen. When the slides were being examined, measurements were made of several hundred pine grains. On a basis of size-frequency studies (Cain 1940), it appears that the smallest of the three fossil species from the buried soils was probably *Pinus banksiana*. If this determination is correct, and present information so indicates, jack pine is as good an indicator of the changed climate as spruce and fir, and these genera offer mutual corroboration. The pine with the small pollen has a considerable representation: 61 per cent at Station I (spectrum 10), 17 per cent at Station II (spectrum 6), 10 per cent at Station IV (spectra 2 and 9), and 12 per cent at Station VIII (spectrum 7). This species occurs generally at all levels in moderate amounts without indicating any discernible trend. Its strong representation at Station I appears to be exceptional. Furthermore, the idea of long distance dissemination which must be considered for spruce and fir is even more untenable for jack pine. Today it does not grow natively closer to Spartanburg, so far as published records reveal, than northern New York and northern Indiana. It is not known, of course, where this pine grew during the period of sedimentation, nor why it should have been completely eliminated from the area, but there is no pine known at present in the southeast with pollen grains so small. Sandy habitats are not abundant in the southern highlands, and an ameliorating climate might have resulted in rather rapid succession and the elimination of a species like jack pine through the competition of climax dominants.

In addition to the above conifers, it should also be noted that *Tsuga* is

today alien to the prevailing climate, and that the more mesophytic trees (*Fagus*, *Betula*, etc.) are confined, as postclimax relics, to protected ravines and slopes. Finally, the presence of *Sphagnum* spores in each buried soil, and their considerable numbers at Station I, are in accord with the preceding interpretations.

With respect to these considerations, I believe a reconstruction of the vegetation during the time of sedimentation would be somewhat as follows. The characteristic upland climax, probably occupying the largest acreage, was oak-hickory-chestnut. This climax was probably interrupted in many places by pine scrubclimax—on drier, rockier, upper slopes and, especially, where fires had destroyed the climax. Generally through the area, but especially in the ravines and on the protected slopes of the stream systems, occurred the mixed mesophytic forests playing, even at this time, a post-climax role. Finally, on the local ponds where the buried soils accumulated, there probably grew most of the spruce and fir. They probably occurred as bog-mat species and on the cooler slopes adjacent to the ponds. The general picture, then, is not much different from that which probably prevailed before man and his agriculture except that the climate was sufficiently cooler, especially in the earlier part of the period, to have supported spruce-fir, jack pine, etc., now absent. How much cooler it is not possible to say, since these cool-climate elements already occurred solely as relics out of harmony with the prevailing conditions and depending for their survival upon edaphic and microclimatic conditions.

Returning to the question of the identification of species in fossil floras, there are certain points that must be emphasized. Specifically, it can not be assumed as proven that the Spartanburg sediments contain pollen of *Pinus banksiana*. It has been shown only that certain abundant small grains in the sediments resemble closely grains of that species. The grains of *Abies* are likewise of special interest. It was at first assumed, and reasonably so, that the fir pollen of the sediments was *Abies Frascri*, the modern species of the high southern Appalachians. A recent study (Cain 1944), however, has shown that the fossil fir pollen does not correspond in size with *Abies Frascri* or *A. balsamea*, but is very much larger and more like the western *A. nobilis* (Wodehouse 1935). Although such a study does not serve to identify the fossil *Abies*, it does away with what would otherwise appear to have been a logical guess as to its identity. Perhaps the fir pollen is that of an extinct species rather than of one that is now geographically far distant. In the same manner, the small-grained pine may be an extinct species, rather than the far-northern jack pine. In any case, we are given a suggestion that the buried soils are possibly of greater age than early post-Wisconsin, for it is unusual for post-Wisconsin sediments to contain extinct species, or for ex-

tant species to have withdrawn their areas such great distances as would be required in the case of this pine and fir.³

Attention must also be given to certain other aspects of the profiles. At Station I the oak-hickory-chestnut complex shows a consistent rise and decline from the bottom to the top of the buried soil, with a maximum of about 35 per cent in the spectrum of level number four. This curve is paralleled by a similar but weaker one for the combined mesophytes. No such simple curve is apparent in the other profiles. At Station IV there is a rather steady representation of the oak-hickory-chestnut complex of about 20 per cent in the lower half, with a generally progressive increase in the upper half to a maximum of 63 per cent at the top. This trend is not reflected by the mesophytes. At Station II, however, there is definite evidence that the oak-hickory-chestnut complex and the mesophytes show similar sensitivity to changed conditions. At levels 2, 5, 8, and 11 these groups increase together. Similarly, at levels 3, 6, and 9, when oak-hickory-chestnut decreases, the mesophytes do likewise. The correlation is not perfect, however, as can be seen from the tables.

One of the most interesting phenomena of the profiles is revealed at Stations II and VIII where there are abrupt, reciprocal changes in the importance of the pines and the oak-hickory-chestnut climax. For example, at Station II this climax drops from 62 to 24 per cent between levels 2 and 3, from 72 to 14 per cent between levels 5 and 6, and from 47 to 27 per cent between levels 8 and 9. These changes are balanced very largely by increases in the pines from 28 to 69 per cent, 14 to 74 per cent, and 22 to 56 per cent, respectively. This same tendency is shown at Station VIII, but in a less dramatic manner.

Because many pine species play a characteristic role as subclimax dominants following fire, it is suggested as a likely hypothesis that these alternations represent the widespread destruction of the oak-hickory-chestnut climax by fire and its replacement by an abundance of pine. This idea is supported by the presence of burned wood fragments and traces of charcoal at various levels in the sediments. There is no reason to believe, however, that the periods of time between the levels dominated by the oak-hickory-chestnut climax at levels 2, 5, and 8 (Station II) represent the time required for the recovery of the climax after its destruction by fire and replacement by pine. It is entirely unknown how long was required for the accumulation of a unit of sediment, but it is likely that nine inches of the peaty soil required a longer period of time than one cycle of recovery of the climax from fire.

³ An attempt at the specific identification of other fossils such as *Picea*, *Quercus*, *Carya*, etc., in these buried soils is recognized as highly desirable, but I have had no opportunity so far to go beyond the present studies.

So far in the United States there has been only a small number of paleontological studies depending upon pollen analysis made south of the continental moraines. I have materials for the study of other profiles in the Spartanburg area, but there are large numbers of these buried soils elsewhere, and they should be sought through a wider portion of the Piedmont so that a greater abundance of information will be available for correlation studies and attempts at dating. It is hoped also that investigators will devote increasing attention to the possibility of identification of species and the breaking down of the customarily large ecological groupings of pollen grains and spores. The recent study of grass pollen by Keller (1943) is an excellent step in that direction. So far I have made no attempt to utilize macrofossils from these profiles for corroboration and supplementation of the pollen studies, but it should be done when time permits. And not only should pollen analysts supplement their pollen investigations with study of whatever macrofossils may be available: there are famous fossil floras, up to now examined solely on a basis of macrofossils, awaiting examination by enterprising pollen analysts. The work of Wodehouse (1932) on the pollen grains of the Green River flora is the only one of such scope yet made in the United States so far as I know.

SUMMARY

In the Piedmont near Spartanburg, South Carolina, there are numerous small sedimentary basins containing highly organic soils that are buried under several feet of inorganic soil of types generally considered to be completely residual. Pollen analyses of profiles of four of these buried soils indicate that their age is sufficient to relate them to a cooler climate than prevails in the area today and probably to the Pleistocene. Pollen grains of *Picea* and *Abies* are more abundant in the lower half of the deposits, a fact that provides an indication that the sediments accumulated under a warming climate. It is demonstrated that the *Abies* is not one of the modern species of Eastern America, and that one of the pines may be the northern *Pinus banksiana*. On a basis of these data it is concluded that the burial of the soils was probably not associated with accelerated erosion in historical times due to agriculture.

The profiles reveal some indication of repeated destruction of the oak-hickory-chestnut climax by fire, its replacement by pine, and its recovery again to climax conditions.

The general picture of the vegetational pattern of the Spartanburg area during the time of the sedimentation is as follows: The rolling uplands were covered by a climax of oak-hickory-chestnut; ravines and protected slopes contained stands of mixed mesophytes; several places where small streams were impounded postclimax spruce-fir grew on and around bog-like basins;

over the upland the prevailing climax was interrupted by stands of pine and pine-hardwood mixtures representing various stages of secondary succession.

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THE VEGETATION OF PILOT MOUNTAIN, NORTH CAROLINA: A COMMUNITY ANALYSIS¹

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INTRODUCTION

Rising abruptly to a height nearly 1500 feet above its surroundings, Pilot Mountain has long been a landmark in the northwestern Piedmont of North Carolina. Although it is located well within the Piedmont Plateau and is isolated from the Blue Ridge, certain species that are ordinarily found only at high altitudes occur near its summit. These obvious relationships both to the Piedmont and to the mountains proper suggested the desirability of an ecological study, and a phytosociological survey of the vegetation was made in 1941 and 1942.

THE AREA

Pilot Mountain is the most southwestern outpost of the Sauratown Mountains and is located in the southeastern corner of Surry County, North Carolina. Several miles separate it from the two nearest spurs of the Sauratown Range. Except for hills in its immediate vicinity, the 2413 foot peak (Pratt 1917) is isolated and is surrounded by the characteristic gently rolling topography of the Piedmont Plateau.

Topography. The mountain may be separated topographically and vegetationally into two distinct parts. The eastern half is an almost perfect pyramid, which is topped by The Knob, or Big Pinnacle (fig. 1); the western half is an elongated, gently rounded ridge, which, extending westward from its highest point, the Little Pinnacle, is outlined by The Ledge. Both The Ledge and the sides of the two pinnacles are nearly vertical cliffs composed of horizontally stratified rock.

On the north the two sections of the mountain are separated by Grindstone Ridge, which slopes gradually downward from the Little Pinnacle. A third long ridge extends downward from the southeast corner of The Knob, and several shorter ones are found on all exposures. Northwest of the Big Pinnacle, separating it from the Little Pinnacle and from Grindstone Ridge, is a broad cove, which is dissected by several shallow ravines and broad, low ridges. A number of ravines occur on the eastern half of the mountain, but few are found on the western half.

There are several flats at various altitudes on the eastern pyramid. The two largest, both at about 1600 feet, are Hickory Flat, which extends across

¹ Publication of the tables is made possible by a grant from Duke University.

most of the east slope, and Poplar Flat, which covers fifteen or more acres on the south slope.

Geology and Soils. Descriptions which follow are based upon the soil survey of Surry County (Davis and Goldston 1937), the only available record that deals specifically with geology and soils of the area.

Quartzite caps Pilot Mountain, and hornblende schist occurs intermixed with gneiss along its western boundary. At all altitudes small outcrops of

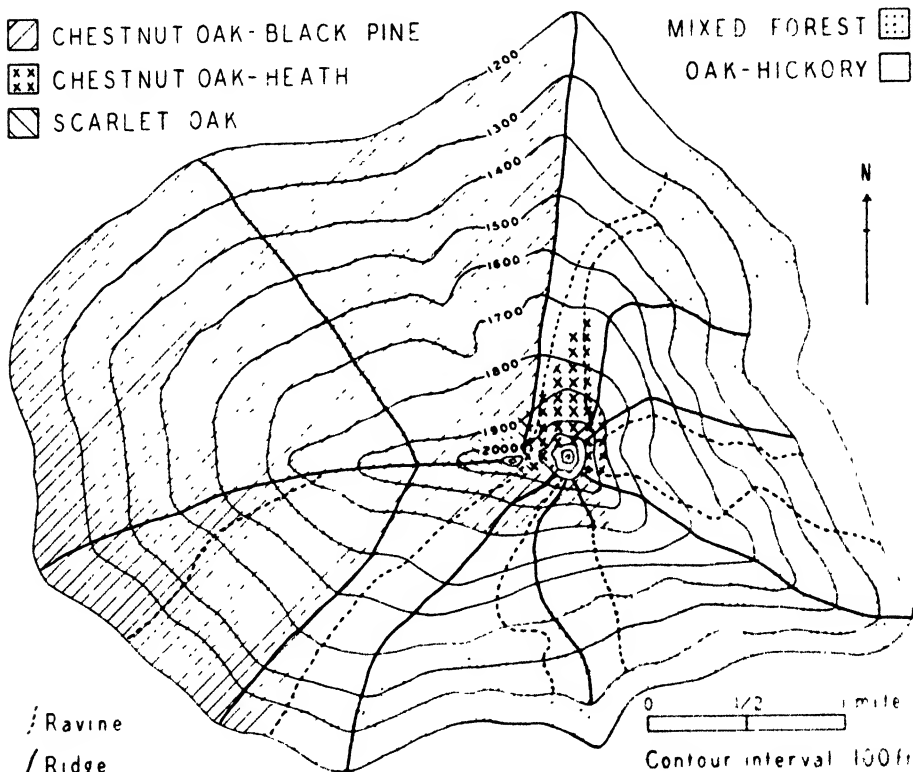


FIG. 1. Rough contour map of Pilot Mountain showing positions of transect lines and general extent of each major plant community. Contours adapted from Book 69, office of Register of Deeds, Dobson, N. C.

quartzite are numerous, and many slabs are scattered over the surface. The soils are derived from the underlying quartzite. Hartsells stony fine sandy loam occurs at the lower altitudes, and its steep phase, interrupted by rock ledges and outcrops, covers the steeper slopes. On gentle slopes the surface soil (A horizon) is from 5 to 8 inches thick and is a light gray to grayish-yellow fine sandy loam. In places organic accumulation produces a brown color. The subsoil (B horizon) is a pale yellow or grayish-yellow friable fine

sandy loam which grades into the yellow, disintegrated quartzite at a depth ranging from 15 inches to 4 feet. On the steep slopes and on most of the western half of the mountain the veneer of soil is very thin. A restricted area on the north slope below The Knob has a red soil with a brown surface (Hanceville).

Climate. The nearest weather station is at Mount Airy, which is some twenty miles from Pilot Mountain and which has an altitude of only 1048 feet. The average annual precipitation there is 46.69 inches, with the greatest rainfall recorded for the summer months and the least, for November. The mean annual temperature is 56.9° F. Monthly averages vary from 75.3° F for July to 38.0° F for January. Other stations in this section have similar records with very minor variations.

Although climatological data are not available from The Pilot itself, or from a comparable locality in its vicinity, it is only logical to assume that the precipitation and temperature on the mountain follow the same monthly trends as those recorded at nearby stations; but that the precipitation is somewhat greater on the mountain, while the temperature is slightly less. The growing season is also evidently less than the average frost-free season of 175 days recorded at Mount Airy.

History. Exploitation of the resources and scenery of Pilot Mountain has been attempted by its several owners with but meager success. At times every tree of merchantable size has been cut for lumber. Recently, however, the only cutting has been of cordwood from around the base. Several orchards and cleared fields are found on the lower slopes, and there are indications that a number of others once existed but have been abandoned. As recently as 1930, a field was cleared on top of The Ledge, but it was abandoned after a few years of unsuccessful cultivation.

Teresa Gilliam, for whom the mountain and surrounding lands were held in trust from 1826 to 1870, seems to have realized that the chief values of The Pilot are scenic. She had a trail constructed on the south side of the mountain and ladders on the side of The Knob. No further serious attempt to commercialize the mountain was made until 1929, at which time Mr. Spoon built wooden steps on the north side of the Big Pinnacle and constructed a toll road from the base of the mountain on the northeast to the summit of the Little Pinnacle.

Fire occurred very regularly in the past and resulted in extensive burned-over areas. The most serious recent fire burned over most of the mountain in 1927, and practically all of the large trees are badly fire-scarred. Since the construction of the toll road, however, only two small fires have occurred.

METHODS

The known collections from Pilot Mountain include 303 species of vascular plants representing 76 families. Collections of mosses, though incomplete, include 55 species representing 16 families. All these specimens are deposited in the herbarium of Duke University.

A statistical study was based upon 158 sample areas (stations), which were spaced at altitudinal intervals of 100 feet along lines (fig. 1) ascending 9 slopes and 8 ravines. Although the samples were taken at intervals the vertical lines were considered as modified transects. At each station estimates were made of *abundance*, *coverage*, *size classes*, and *sociability* of each species on an area approximately 50 feet square. The transect plan was originally used because altitudinal variation in the vegetation was anticipated. However, when the results had been tabulated and compared with habitat notes taken at each station, it was found that four general plant communities exist on Pilot Mountain. The limits of these communities were defined (fig. 1), and the data were separated accordingly. From these statistics a sociological summary of each community was made.

In general, the terminology used is that which was summarized by Cain (1932). The vertical "transect" lines were treated as stands and the altitudinally spaced stations were used as sample areas within the stands. The average frequency of each species within a community was obtained by averaging the frequency values for that species from all "transects" or portions of "transects" that fell within the boundaries of the community under consideration. The results are expressed in percentages. Similarly, values for abundance and coverage were averaged. These values, however, are expressed by means of classes. For abundance, the 5 classes suggested by Cain (1932) were used. For coverage, a class was added for the species that occupy less than one per cent of the surface; thus giving the following arrangement:

- C 0, species covering less than 1 per cent of the surface.
- C 1, species covering 1-5 per cent of the surface.
- C 2, species covering 6-25 per cent of the surface.
- C 3, species covering 26-50 per cent of the surface.
- C 4, species covering 51-75 per cent of the surface.
- C 5, species covering 76-100 per cent of the surface.

The five size classes that were recognized are:

- S 1, species found in the ground cover.
- S 2, herbs and shrubs below one foot in height.
- S 3, shrubs and transgressives below 8 feet in height.
- S 4, trees of the understory.
- S 5, trees of the upperstory.

Presence is expressed as a percentage which indicates the ratio of the number of stands ("transects") in which the species occurred to the number

of "transects" placed within the community. The values for constancy are based upon the total number of sample areas (stations) which were studied in a community. Five classes of constancy are recognized and those species which occurred at more than 80 per cent of the stations (class 5) are considered to be constants. The classes are as follows:

- Co 1, species occurring in 1-20 per cent of the examples.
- Co 2, species occurring in 21-40 per cent of the examples.
- Co 3, species occurring in 41-60 per cent of the examples.
- Co 4, species occurring in 61-80 per cent of the examples.
- Co 5, species occurring in 81-100 per cent of the examples.

DESCRIPTION OF COMMUNITIES

Most extensive of the four plant communities on Pilot Mountain is the *chestnut oak—black pine* community of the western half of the mountain and the upper south slopes. This gradually changes into the *chestnut oak—heath* of the higher east and north slopes. Richest and most heterogeneous of the four is the *oak-hickory* forest of the middle altitudes and ravines on the south, the east, and the north-facing slopes that lie below The Knob. The *mixed forest* occupies the lower slopes of these exposures. Because of its position and peculiar flora the *top of The Knob* is treated separately.

Chestnut Oak—Black Pine Community. Except for ravines, this community occupies all the area from Grindstone Ridge westward around the mountain to that ravine on the south which separates the two pinnacles. It also continues across that part of the south-facing slope which roughly lies between an altitude of 1800 feet and The Knob, and gradually gives way to the chestnut oak—heath (fig. 1).

Most of this region has a gently rounded slope with but few ridges and ravines. A thin layer of soil only partially covers the rocky surface, and the poor quality of the site is reflected in the vegetation. The trees are poorly developed and form an open canopy, while the shrubs and herbs are scattered and frequently appear stunted.

Data from 61 stations distributed along 11 "transects" are summarized in table 1. These show seven constants: *Quercus montana*¹ and *Pinus rigida* in the tree layer, *Quercus marilandica* and *Oryzodendrum arborum* in the understory, *Vaccinium vacillans* and *Kalmia latifolia* in the shrub layer, and *Andropogon* spp. in the herb layer. If *Nyssa sylvatica*, chiefly an understory species whose frequency is 87 per cent, were included with the seven constants, this list would contain all species with abundance values of 4 or 5, or average frequencies of more than 80 per cent. Except for *Oryzodendrum arborum*, each of these species has a presence of 100 per cent.

¹ Authorities for names are given in the tables the first time each specific name appears.

TABLE 1

Data for Chestnut Oak—Black Pine Community with Stratification (S), Abundance (A), Coverage (C), Frequency (F), Presence (P), and Constancy (Co) for each species

Species	S	A	C	F	P	Co
Usually found in upperstory:						
<i>Quercus montana</i> Willd.	5, 4, 3	5	2	97	100	5
<i>Pinus rigida</i> Mill.	5, 4, 3	5	2	96	100	5
<i>Quercus coccinea</i> Muench.	5, 4, 3	3	1	42	64	3
<i>Pinus virginiana</i> Mill.	5, 4, 3	2	0	17	36	2
<i>Pinus pungens</i> Lam.	5, 4, 3	2	0	18	64	1
<i>Quercus velutina</i> Lam.	5, 4	2	0	9	36	1
<i>Quercus alba</i> L.	5, 4	1	0	6	18	1
<i>Pinus echinata</i> Mill.	5, 4	1	0	3	18	1
<i>Liriodendron tulipifera</i> L.	5, 4, 3	1	0	1	18	1
Usually found in understory:						
<i>Quercus marilandica</i> Muench.	4, 5, 3	4	1	84	100	5
<i>Oxydendrum arboreum</i> (L.) DC.	4, 3, 5	4	1	94	91	5
<i>Nyssa sylvatica</i> Marsh.	4, 3, 5	4	1	87	100	4
<i>Robinia pseudo-acacia</i> L.	4, 2, 5	2	1	44	100	3
<i>Sassafras albidum</i> (Nutt.) Nees	4, 3, 2	2	0	51	82	3
<i>Acer rubrum</i> L.	4, 3, 5	2	1	39	82	3
<i>Carya alba</i> (L.) Koch, <i>C. glabra</i> (Mill.) Spach., <i>C. pallida</i> (Ashe) Sarg.	4, 3, 5	2	0	30	73	2
<i>Castanea dentata</i> (Marsh.) Borkh.	4, 3	2	0	34	64	2
<i>Hamamelis virginiana</i> L.	4, 3	1	0	6	36	1
<i>Amelanchier canadensis</i> (L.) Medic.	4	1	0	4	27	1
<i>Quercus borealis</i> Michx. var. <i>maxima</i> (Marsh.) Ashe	4	1	0	1	18	1
Shrub layer:						
<i>Vaccinium</i> spp.	2, 3	5	1	99	100	5
<i>Kalmia latifolia</i> L.	3	4	2	84	100	5
<i>Polycodium stamineum</i> (L.) Greene	3, 2	2	1	45	82	3
<i>Azalea nudiflora</i> L.	3, 2	2	1	33	82	2
<i>Gaylussacia baccata</i> (Wang.) K. Koch.	2, 3	2	1	40	73	2
<i>Diospyros virginiana</i> L.	3, 4	2	0	32	82	1
<i>Epigaea repens</i> L.	1	2	0	23	55	1
<i>Ilex montana</i> (T. and G.) Gray	3	1	0	17	45	1
<i>Ceanothus americanus</i> L.	3, 2	1	0	12	36	1
<i>Quercus ilicifolia</i> Wang.	3	1	0	10	36	1
<i>Lyonia ligustrina</i> (L.) DC.	3	1	0	9	36	1
<i>Comptonia peregrina</i> (L.) Coult.	2	1	0	9	36	1
<i>Robinia hispida</i> L.	2	2	0	8	36	1
<i>Rhododendron catawbiense</i> Michx.	3	1	0	9	27	1
<i>Rubus</i> spp.	3, 2	1	0	6	27	1
<i>Rhus copallina</i> L.	3	1	0	11	18	1
<i>Galax aphylla</i> L.	1	1	0	4	18	1
<i>Rhododendron maximum</i> L.	4	1	0	2	18	1
<i>Rhus glabra</i> L.	3	1	0	2	18	1
<i>Castanea pumila</i> (L.) Mill.	3	1	0	5	9	1
Woody vines:						
<i>Smilax rotundifolia</i> L.	3, 2, 4	3	1	65	100	4
<i>Vitis aestivalis</i> Michx. and <i>V. cordifolia</i> Michx.	4, 3	1	0	1	18	1

TABLE 1 (Continued)

Species	S	A	C	F	P	Co
Herbs:						
<i>Andropogon scoparius</i> Michx. and <i>A. virginicus</i> L.	2	4	1	89	100	5
<i>Pteridium aquilinum</i> (L.) Kuhn, 2 var.	2	3	1	75	100	4
<i>Chrysopsis graminifolia</i> Nutt. var. <i>aspera</i> (Shuttlew.) Gray	2	2	0	67	100	4
<i>Panicum</i> spp.	2	2	0	60	100	3
Leguminosae sp.	2	3	1	63	91	3
<i>Solidago</i> spp.	2	2	0	62	91	3
<i>Tephrosia virginiana</i> (L.) Pers.	2	3	1	59	91	3
<i>Coreopsis major</i> Walt.	2	2	0	38	82	3
<i>Hieracium venosum</i> L.	2	2	0	48	100	2
<i>Iris verna</i> L.	2	2	0	16	45	2
<i>Scriocarpus asteroides</i> (L.) BSP.	2	1	0	12	55	1
<i>Baptisia tinctoria</i> (L.) R. Br.	2	1	0	17	45	1
<i>Houstonia tenuifolia</i> Nutt.	2	2	0	16	45	1
<i>Potentilla</i> spp.	2, 1	1	0	9	34	1
<i>Hypoxis hirsuta</i> (L.) Coville	2	1	0	5	27	1
<i>Viola</i> spp.	2	1	0	4	27	1
<i>Chimaphila maculata</i> (L.) Pursh	2	1	0	3	27	1
<i>Salpium compositum</i> Michx.	2	1	0	3	27	1
<i>Euphorbia corollata</i> L.	2	1	0	3	18	1
<i>Gillenia trifoliata</i> (L.) Moench.	2	1	0	3	18	1
Gramineae sp.	2	1	0	2	18	1
<i>Auricularia</i> spp.	2	1	0	1	18	1
<i>Smilacina racemosa</i> (L.) Desf.	2	1	0	1	18	1
Compositae spp.	2	1	0	7	9	1

NOTE: The following species occurred in only one station and therefore have a constance of two per cent and a presence of nine per cent: *Antennaria* sp., *Aralia spinosa* L., *Asarum* sp., *Asplenium platyneuron* (L.) Oakes, *Galium* sp., *Hypopitys americana* (DC.) Small, *Osmunda cinnamomea* L., *Phoradendron flavescens* (Pursh) Nutt., *Polygonatum biflorum* (Walt.) Ell., *Polypodium virginianum* L., *Polystichum acrostichoides* (Michx.) Schott., and *Saguna decumbens* (Ell.) T. and G.

Sixteen additional species have a presence of more than 80 per cent, but only 8 of these have a cover value of as much as 1 per cent: *Robinia pseudo-acacia* and *Acer rubrum* in the understory; *Polycodium stamineum*, *Azalea nudiflora*, and *Smilax rotundifolia* among the shrubs; *Pteridium aquilinum*, *Tephrosia virginiana*, and several other legumes among the herbs. Of this supplementary list, only *Pteridium aquilinum*, *Smilax rotundifolia*, and the legumes have frequencies that average more than 50 per cent.

Some oaks and pines in the upperstory appear to be dying, and a number of the older oaks are grotesquely gnarled. Of the upperstory species, chestnut oak is by far the most important in lesser strata. Blackjack oak seldom attains upperstory size but often occurs in dense stands. These two oaks dominate the understory and transgressive layers, with sourwood and black gum as important associates. Seedlings of both oaks are numerous, and black locust, though widely scattered in the understory, is often found among the

TABLE 2

Data for Chestnut Oak—Heath Community with Stratification (S), Abundance (A), Coverage (C), Frequency (F), Presence (P), and Constancy (Co) for each species

Species	S	A	C	F	P	Co
Usually found in upperstory:						
<i>Quercus montana</i>	5, 4	5	1	91	100	5
<i>Pinus rigida</i>	5, 4	4	1	69	88	4
<i>Pinus pungens</i>	5, 4, 3	2	0	17	25	2
<i>Quercus borealis</i> var. <i>marima</i>	5, 3	1	0	27	38	1
Usually found in understory:						
<i>Nyssa sylvatica</i>	4, 3	3	1	61	100	4
<i>Castanea dentata</i>	4, 3	3	1	80	88	4
<i>Oxydendrum arboreum</i>	4, 3, 5	3	1	69	88	4
<i>Robinia pseudo-acacia</i>	4, 2	2	0	63	88	3
<i>Acer rubrum</i>	4, 3	2	0	56	75	3
<i>Hamamelis virginiana</i>	4, 3	2	0	54	75	3
<i>Sassafras albidum</i>	4, 3	3	1	48	75	3
<i>Carya</i> spp.	4	1	0	27	38	1
<i>Amelanchier canadensis</i>	4	1	0	13	25	1
Shrub layer:						
<i>Kalmia latifolia</i>	3, 4	5	2	100	100	5
<i>Rhododendron catawbiense</i>	3, 4	4	1	83	100	5
<i>Vaccinium</i> spp.	3, 2	4	1	71	100	5
<i>Epigaea repens</i>	1	3	1	76	100	4
<i>Gaylussacia baccata</i>	3, 2	4	1	72	100	4
<i>Lyonia ligustrina</i>	3	2	0	52	75	3
<i>Galax aphylla</i>	1	3	1	45	75	3
<i>Leucothoe recurva</i> (Buckl.) A. Gray	3	2	0	35	75	2
<i>Quercus ilicifolia</i>	3	2	0	35	75	2
<i>Polycodium</i> spp.	3	2	0	30	63	2
<i>Pieris floribunda</i> (Pursh) Benth. & Hook	3	2	1	21	25	2
<i>Azalea nudiflora</i>	3	2	0	25	38	1
<i>Ilex montana</i>	3	1	0	17	38	1
<i>Aronia melanocarpa</i> (Michx.) Ell.	3	1	0	14	38	1
<i>Comptonia peregrina</i>	2	1	0	10	25	1
Woody vine:						
<i>Smilax rotundifolia</i>	3	2	0	27	50	2
Herbs:						
<i>Pteridium aquilinum</i> , 2 var.	2	2	0	44	75	3
<i>Solidago</i> spp.	2	2	0	46	88	2
<i>Andropogon</i> spp.	2	2	0	43	38	1
<i>Chrysopsis graminifolia</i> var. <i>aspera</i>	2	1	0	23	38	1
<i>Osmunda cinnamomea</i>	2	2	0	21	38	1
<i>Iris verna</i>	2	1	0	23	38	1
<i>Baptisia tinctoria</i>	2	1	0	23	25	1
Gramineae sp.	2	1	0	17	25	1
Leguminosae spp.	2	1	0	17	25	1
<i>Panicum</i> sp.	2	1	0	17	25	1
<i>Deschampsia flexuosa</i> (L.) Trin.	2	1	0	16	25	1
<i>Chimaphila maculata</i>	2	1	0	14	25	1
<i>Polystichum acrostichoides</i>	2	1	0	14	25	1
<i>Serriocarpus asteroides</i>	2	1	0	13	25	1
<i>Asarum</i> sp.	2	1	0	10	25	1
<i>Aureolaria</i> spp.	2	1	0	10	25	1

TABLE 2 (Continued)

Species	S	A	C	F	P	Co
<i>Paronychia argyrocoma</i> (Michx.) Nutt.	2	1	0	10	25	1
<i>Polypodium virginianum</i>	2	1	0	10	25	1
<i>Gillenia trifoliata</i>	2	1	0	6	25	1
<i>Dioscorea glauca</i> Muhl.	2	1	0	8	13	1

NOTE: The following species occurred in only one station and therefore have a constance of five per cent and a presence of thirteen per cent: *Asplenium platyneuron*, *Athyrium asplenoides* (Michx.) Desv., *Diospyros virginiana*, *Euphorbia corollata*, *Goodera pubescens* R. Br., *Heuchera* sp., *Hieracium venosum*, *Houstonia tenuifolia*, *Hydrangea arborescens* L., *Liriodendron tulipifera*, *Polygonatum biflorum*, *Pyrus malus* L., *Quercus coccinea*, *Quercus marilandica*, *Smilacina racemosa*, *Steironema intermedium* Kearney, *Tephrosia virginiana*, and *Viola pedata* L.

seedlings. Sassafras is important in the understory on the higher south slopes. Although colonies of young pines frequently occur in openings, pine, when the entire area is considered, is of less importance in the lower strata than are the hardwoods. The shrub layer is composed chiefly of huckleberries, laurel, and transgressives. It seems to be better developed on north-facing than on south-facing slopes, and its importance also increases with altitude. Scattered herbs are present everywhere except in the dense stands of black-jack oaks.

The greatest variation in the community occurs in the triangular area that lies between Grindstone Ridge and The Ledge. Here scarlet oak not only replaces blackjack oak but in places almost crowds out chestnut oak and pine. Since the area concerned is small, and since the subordinate species are not different, this evidently constitutes a local variation of the chestnut oak—black pine community.

Minor local variations are related to more favorable moisture conditions. In such places service berry, rhododendron, mountain holly, bear oak, galax, and cinnamon fern may be found, while the usual shrubs are larger and more abundant. In crevices and pockets on the rock cliffs that form the sides of the two pinnacles and The Ledge, are found certain species that are seldom seen elsewhere on the mountain; namely, *Asplenium montanum* Willd., *Heuchera parviflora* Bartl. var. *typica* R. B. and L., *Sagina decumbens*, and *Paronychia argyrocoma*. Along with these are various other plants, even dwarf trees.

Chestnut Oak—Heath. The chestnut oak—heath extends along both east and north-facing slopes immediately below The Knob but reaches its best development at the north base and down a shallow ravine on the north side (fig. 1). Although scattered ericads may be present in the shrub layer at lower altitudes, their occurrence in thickets is infrequent below an elevation of 1900 feet. The ravine on the north is an exception, for there the heath

thicket extends downward almost 200 feet farther than its usual limit. Throughout most of the area occupied by this community the slope is steep and rocky, with thin soil and litter only in spots.

Vegetational statistics were secured from 20 stations distributed along 8 "transects." The data (table 2) show that the constants, in order of their decreasing abundance and frequency are: *Kalmia latifolia*, *Quercus montana*, *Rhododendron catawbiense*, and species of *Vaccinium*. The first three are the only species in this community with average frequencies of over 80 per cent, but each constant has a presence of 100 per cent. Since the shrubs are more abundant than the trees and have a greater coverage, in places approaching 100 per cent, and since 7 of the 12 shrubs that have frequencies of more than 20 per cent are ericads; the name "chestnut oak—heath" seems most appropriate for the community.

In general, the physiognomy is that of dwarfed, widely spaced trees above a dense thicket of shrubs and trees that are scarcely taller than the shrubs. Chestnut oak is the dominant tree, but clusters of pine occur in places where the laurel and rhododendron are replaced by huckleberries. All the trees are of fair size at lower altitudes but rapidly decrease in number, size, and quality as The Knob is approached. At the base of The Knob, the trees are dwarfed, and the shrubs are frequently from 8 to 12 feet high, while understory species are but slightly taller than the shrubs. This makes the three strata almost the same height.

In the understory is a greater number of chestnut sprouts than is found in any other community. Sourwood, black gum, and sassafras are fairly abundant. Transgressives and seedlings of tree species are found in openings only, but seedlings of the shrub species are fairly abundant everywhere. The larger rocks form practically the only bare places, and even these are often partially or entirely obscured by the ericads. Laurel and rhododendron grow in clumps with many sprouts from the roots. Where these clumps are close together a true thicket is formed; where they are more widely spaced the other shrubs are usually as dense but not so tall as these two species. Bear oak forms its own thickets, which are evenly distributed through the upper altitudes. Huckleberries cover whatever space is left between the other shrubs and fill all openings in the thickets. Beneath all else is a carpet of galax or, at lower altitudes, trailing arbutus. Bracken fern is found here and there, but herbs are of little importance except in the paths.

Altitudinal zonation is apparent in the distribution of the shrubby plants of the community. The number of shrub species increases upward. At lower altitudes, varying from about 1725 feet in the north ravine to 1950 feet on the east, azalea, laurel, and huckleberries are the most important shrubs. Rhododendron and trailing arbutus enter at slightly higher altitudes; galax becomes abundant about 100 feet above the first colonies of

arbutus; and bear oak occurs still higher on the slope. Four species are found only in the chestnut oak—heath. *Leucothoe recurva* occurs for a short distance below The Knob, but *Pieris floribunda*, *Vaccinium corymbosum* L. var. *pallidum* (Ait.) Gray and *Aronia melanocarpa* are limited to the north base of The Knob and to its top. The *Pieris* is so abundant around the northwest base of The Knob that it is dominant, with a coverage of over 50 per cent.

Oak-Hickory Forest. This forest occupies middle slopes on the eastern half of the mountain and most ravines on all exposures. On the south-facing slopes, the transition from the lower mixed forest to oak-hickory coincides with a sudden increase in degree of slope at an altitude of about 1500 feet. The upper limit on this side is an abrupt transition to the chestnut oak—black pine community at about 1800 feet. On the east and north, the community extends from the chestnut oak—heath downward almost to the base of the mountain, where it is interrupted by agricultural land.

The topography is variable. Included are several flats, and drainage lines range from slight depressions to steep-walled ravines. In some areas the soil is deep and is rich in humus; in others, there are piles of nearly bare rock.

The diversity of conditions is reflected in the large number of species, 140 in all, listed from the 61 stations in 13 stands (table 3). *Robinia pseudo-acacia*, with a frequency of 94 per cent, is the only constant; but *Vitis aestivalis*, which is the usual grape (frequency 80 per cent), probably deserves the same rating. When combined, oaks have a constancy of 95 per cent, and hickories of 90 per cent. *Liriodendron tulipifera* (frequency 80 per cent) is probably the most abundant single species in the community. It is local in occurrence, however, and cannot be considered a constant. An almost pure stand occupies about fifteen acres on Poplar Flat; the species is often dominant in the ravines; and small groups are scattered over the slopes, seemingly without design. In general, it is more common on south-facing slopes than on the east or north.

Among the oaks, chestnut oak is most important, having an abundance of 4 and an average frequency of 73 per cent. It becomes the dominant species at higher altitudes, particularly on the east and north. There the oaks are regularly and widely spaced and attain their best development. Northern red oak (frequency 64 per cent) is usually found in moister sites, while white oak (frequency 62 per cent) is more abundant in drier sites.

The understory is usually dense, and its most important species are transgressives that vary with the local dominants. Scattered among these, however, are other species, whose identities also vary with the sites. Sourwood, red maple, chestnut sprouts, and dogwood are more abundant on the east and north-facing slopes than on the south. Black gum, black locust, and per-

TABLE 3

Data for Oak—Hickory Community with Stratification (S), Abundance (A), Coverage (C), Frequency (F), Presence (P), and Constancy (Co) for each species

Species	S	A	C	F	P	Co
Usually found in upperstory:						
<i>Carya</i> spp.	5, 4, 3	4	1	97	100	5
<i>Robinia pseudo-acacia</i>	5, 4	4	1	94	100	5
<i>Liriodendron tulipifera</i>	5, 4, 3	4	1	80	100	4
<i>Quercus montana</i>	5, 4, 3	4	1	73	100	4
<i>Quercus borealis</i> var. <i>maxima</i>	5, 4, 3	3	1	64	100	4
<i>Quercus alba</i>	5, 4, 3	3	1	62	100	3
<i>Juglans nigra</i> L.	5, 4	2	0	52	92	3
<i>Pinus virginiana</i>	5, 4	1	0	13	46	3
<i>Quercus velutina</i>	5, 4	1	0	15	54	1
<i>Pinus rigida</i>	5, 4	1	0	11	31	1
<i>Pinus echinata</i>	5, 4	1	0	7	23	1
<i>Pyrus communis</i> L.	5	1	0	1	8	1
Usually found in understory:						
<i>Nyssa sylvatica</i>	4, 5, 3	3	0	65	100	4
<i>Diospyros virginiana</i>	4, 3	1	0	48	92	3
<i>Oxydendrum arborescens</i>	4, 3, 5	2	0	53	85	3
<i>Cornus florida</i> L.	4, 5, 2	3	0	52	85	3
<i>Acer rubrum</i>	4, 5	2	0	50	85	3
<i>Castanea dentata</i>	4, 5	2	0	34	70	3
<i>Fraxinus americana</i> L. and <i>F. biltmoreana</i> Beadle	4, 5	2	0	58	62	3
<i>Cercis canadensis</i> L.	4, 5	2	0	35	62	2
<i>Ulmus fulva</i> Michx.	4, 5	2	0	22	46	2
<i>Morus rubra</i> L.	4, 3	1	0	11	38	1
<i>Viburnum prunifolium</i> L.	4	1	0	7	38	1
<i>Prunus serotina</i> Ehrh.	4, 3	1	0	5	23	1
Shrub layer:						
<i>Hydrangea arborescens</i>	3, 2	3	1	53	70	4
<i>Rubus</i> spp.	3, 2	2	0	39	92	3
<i>Rhus toxicodendron</i> L. and var. <i>radicans</i> (L.) Torr.	2, 3	2	0	39	77	2
<i>Sassafras albidum</i>	3, 2	2	0	24	62	2
<i>Azalea nudiflora</i>	3	2	0	31	54	2
<i>Ceanothus americanus</i>	2, 3	1	0	18	62	1
<i>Kalmia latifolia</i>	3, 2	1	0	19	46	1
<i>Vaccinium vacillans</i> Kalm	2, 3	2	0	22	38	1
<i>Chionanthus virginica</i> L.	3, 4	1	0	11	31	1
<i>Polycodium stamineum</i>	3	1	0	6	31	1
<i>Viburnum acerifolium</i> L.	3	1	0	8	23	1
<i>Alnus rugosa</i> (Ehrh.) Spreng.	3	1	0	4	15	1
<i>Rhus copallina</i>	3	1	0	4	15	1
<i>Hamamelis virginiana</i>	3	1	0	5	8	1
<i>Epigaea repens</i>	1	1	0	1	8	1
Woody vines:						
<i>Vitis</i> spp.	4, 1, 3, 5	3	1	80	100	5
<i>Parthenocissus quinquefolia</i> (L.) Planch.	1, 3, 4	3	1	67	100	4
<i>Smilax</i> spp.	2, 4, 3	2	0	24	62	2
<i>Tecoma radicans</i> (L.) Juss.	3, 2, 4	1	0	6	23	1

TABLE 3 (Continued)

Species	S	A	C	F	P	Co
Herbs:						
<i>Cimicifuga racemosa</i> (L.) Nutt.	2	3	1	67	100	4
Leguminosae spp.	2	3	0	65	100	4
<i>Galium</i> spp.	2	3	0	58	100	4
<i>Polystichum acrostichoides</i>	2	3	1	65	85	4
<i>Panicum</i> spp.	2	2	0	50	92	3
<i>Viola</i> spp.	2	2	0	49	92	3
<i>Arisaema triphyllum</i> (L.) Schott	2	3	1	57	85	3
Compositae spp.	2	2	1	48	85	3
<i>Heuchera</i> spp.	2	2	0	39	85	3
<i>Smilacina racemosa</i>	2	2	0	51	77	3
<i>Asplenium platyneuron</i>	2	2	0	36	92	2
<i>Trillium catesbaei</i> Ell.	2	2	0	32	92	2
<i>Chimaphila maculata</i>	2	2	0	39	85	2
<i>Botrychium virginianum</i> (L.) Sw.	2	2	0	31	85	2
<i>Solidago</i> spp.	2	2	0	34	77	2
<i>Euphorbia corollata</i>	2	2	0	29	77	2
<i>Coreopsis major</i>	2	1	0	21	77	2
<i>Sanguinaria canadensis</i> L.	2	2	1	30	62	2
<i>Urtica perfoliata</i> L. and <i>U. sessili-</i> <i>folia</i> L.	2	2	0	28	62	2
<i>Dioscorea glauca</i>	2	2	0	25	62	2
<i>Circaea latifolia</i> Hill	2	2	0	24	62	2
<i>Sanicula canadensis</i> L.	2	1	0	24	62	2
<i>Adiantum pedatum</i> L.	2	2	0	23	62	2
<i>Andropogon</i> spp.	2	2	0	23	54	2
<i>Athyrium asplenoides</i>	2	2	0	20	70	1
<i>Pteridium aquilinum</i> , 2 var.	2	1	0	17	54	1
<i>Hieracium venosum</i>	2	1	0	15	54	1
Gramineae spp.	2	1	0	14	54	1
<i>Bromus purgans</i> L.	2	2	0	23	46	1
<i>Impatiens biflora</i> Walt.	2	2	0	16	46	1
<i>Houstonia tenuifolia</i>	2	1	0	14	46	1
<i>Agrimonia</i> spp.	2	1	0	12	46	1
<i>Phryma leptostachya</i> L.	2	1	0	11	46	1
<i>Aruncus dioicus</i> (Walt.) Fernald	2	1	0	9	38	1
<i>Antennaria</i> spp.	2	1	0	12	31	1
<i>Silene virginica</i> L.	2	1	0	7	31	1
<i>Thalictrum revolutum</i> DC.	2	1	0	7	31	1
<i>Phytolacca americana</i> L.	2	1	0	5	31	1
<i>Osmunda cinnamomea</i>	2	1	0	10	23	1
<i>Anemone virginiana</i> L.	2	1	0	9	23	1
<i>Erigeron ramosus</i> (Walt.) BSP.	2	1	0	9	23	1
<i>Scutellaria ovalifolia</i> Pers.	2	1	0	9	23	1
<i>Ambrosia elatior</i> L.	2	1	0	7	23	1
<i>Aureolaria</i> spp.	2	1	0	7	23	1
<i>Chrysopsis graminifolia</i> var. <i>asper</i>	2	1	0	7	23	1
<i>Dryopteris hexagonoptera</i> (Michx.) C. Chr.	2	1	0	7	23	1
<i>Iris verna</i>	2	1	0	6	23	1
<i>Woodсия obtusa</i> (Spreng.) Torr.	2	1	0	6	23	1

TABLE 3 (Continued)

Species	S	A	C	F	P	Co
<i>Oxalis europaea</i> Jordan var. <i>bushii</i>						
Small	12	1	0	5	23	1
<i>Steironema intermedium</i>	12	1	0	5	23	1
<i>Athyrium thelypteroides</i> (Michx.) Desv.	12	1	0	8	15	1
<i>Podophyllum peltatum</i> L.	12	1	0	7	15	1
<i>Hypoxis hirsuta</i>	12	1	0	6	15	1
<i>Silphium compositum</i>	12	1	0	5	15	1
<i>Pycnanthemum</i> sp.	12	1	0	4	15	1
<i>Carex</i> sp.	12	1	0	3	15	1
<i>Gillenia trifoliata</i>	12	1	0	3	15	1
<i>Goodyera pubescens</i>	12	1	0	3	15	1
<i>Hypericum</i> sp.	12	1	0	3	15	1
<i>Lilium carolinianum</i> Michx.	12	1	0	3	15	1
<i>Lobelia spicata</i> Lam.	12	1	0	3	15	1
<i>Deschampsia flexuosa</i>	12	1	0	3	8	1
<i>Fragaria virginiana</i> Duchesne	12	1	0	3	8	1
<i>Oenothera fruticosa</i> L.	12	1	0	3	8	1
<i>Polypodium polypodioides</i> (L.) Hitchc.	2	1	0	3	8	1
<i>Saxifraga virginiana</i> Michx.	12	1	0	3	8	1

NOTE: The following species occurred in only one site and therefore have a constancy of two per cent and presence of eight per cent: *Asarum* sp., *Asclepias tuberosa* L., *Ascyrum hypericoides* L., *Baptisia tinctoria*, *Benzoïn acutiale* (L.) Nees, *Betula nigra* L., *Clematis* sp., *Dennstaedtia punctilobula* (Michx.) Moore, *Dryopteris marginalis* (L.) A. Gray, *Elephantopus tomentosus* L., *Eupatorium album* L., *Geum virginianum* L., *Hypopitys americana*, *Ilex montana*, *Ipomoea* sp., *Juniperus virginiana* L., *Lyonia ligustrina*, *Luzula echinata* (Small) Hermann; *Phoradendron flavescens*; *Pinus strobus* L., *Plantago lanceolata* L., *Polygonatum biflorum*, *Polypodium virginianum*, *Prunus persica* (L.) Stokes, *Rumex obtusifolius* L., *Salix nigra* Marsh., *Schrankia angustata* T. and G., *Scleria triglomerata* Michx., *Taraxacum palustre* (Lyons) Lam. and DC. var. *vulgare* (Lam.) Fern., *Tephrosia virginiana*, *Verbascum thapsus* L.

simmon are rather evenly distributed. On the east and north, red bud is more often found in ravines, while on the south it is more frequent on the slopes.

Except for transgressives and woody vines, the shrub layer is not well developed. Chestnut oak seems to be the most abundant tree species among both transgressives and seedlings. The other oaks and the hickories are also abundant in these strata, and seedlings of all the important hardwoods are present. It is the woody vines, however, that give the community its greatest unity. Grape and Virginia creeper are almost never seen outside the borders of the oak-hickory forest; but within it the presence of one or the other, or both, is 93 per cent (57 of 61 stations).

The herb layer is especially rich and varied, herbs being fairly numerous even in the most rocky places. On the moist flats and in those ravines in which the litter is not too thick, this stratum accounts for more than 75 per cent of the cover. The most widely and evenly distributed species is *Cimicifuga racemosa*, which has a frequency of 67 per cent. *Arisaema triphyllum*,

Smilacina racemosa, *Galium* spp., and species of legumes are important in moister sites. Ferns are abundant except in the driest sites. Though *Polystichum acrostichoides* (frequency 65 per cent) is the most uniformly distributed fern, other species frequently occur and often form fairly large colonies. On Poplar Flat and at lower altitudes on the south-facing slopes, a few species of composites dominate the herbaceous layer. The most important of these are *Polymnia canadensis* L., *P. uvedalia* L., *Verbesina occidentalis* (L.) Walt., *Parthenium integrifolium* L., and *Helianthus atrorubens* L.

Mixed Fores. Although interrupted by fields, orchards, pastures, and sites from which fire wood is cut each year, the mixed forest found near the base of the mountain (fig. 1) is not entirely a product of these disturbances. It is therefore included as a community. The soil is very stony and contains little humus. The slope is gradual, with broad, rounded ridges that are dissected by winding ravines.

Data from 16 stations taken from 5 stands (table 4) show that six of the seven constants are found in the upperstory, dwarfed *Vaccinium vacillans* being the seventh (frequency 76 per cent). All other shrubs have frequencies of less than 50 per cent. Constants among the trees are *Quercus montana* (frequency 90 per cent), species of *Carya* (combined frequency 93 per cent), *Pinus virginiana* (frequency 89 per cent), *Quercus alba* (frequency 89 per cent), *Quercus velutina* (frequency 83 per cent), and *Robinia pseudo-acacia* (frequency 79 per cent). *Quercus montana* is the only species in this community with an abundance value of 5. *Nyssa sylvatica* and *Oxydendrum arborescens*, with frequencies of 70 per cent, and *Quercus marilandica* (frequency 56 per cent) are the only other trees of importance. A few herbs have relatively high frequencies (50 to 75 per cent), but all are so widely spaced that their coverage is always less than 1 per cent.

The physiognomy is typical of dry, wooded hillsides in the upper Piedmont and offers a decided contrast to the richer oak-hickory forest higher up the slopes. Except for a few pines in openings, most species in the understory are hardwoods. Seedlings are chiefly oaks and hickories.

Top of the Knob. About one acre of comparatively flat land is found on top of The Knob. This is covered with large, angular slabs of quartzite. In the almost flat central area, chestnut oak is clearly dominant, but near the edge of the cliff this species is replaced by pine. *Pinus pungens* is most abundant at the very margin, while *Pinus rigida* occurs a little farther from the rim. *Oxydendrum arborescens*, *Nyssa sylvatica*, *Acer rubrum*, *Quercus borealis* var. *maxima*, and *Robinia pseudo-acacia* are present in the understory.

The shrub layer of the central area is dominated by ericads. On the west and north is a heath thicket in which the most important species, in order of their decreasing abundance, are: *Pieris floribunda*, *Kalmia latifolia*, *Rhodo-*

TABLE 4

Data for Mixed Forest with Stratification (S), Abundance (A), Coverage (C), Frequency (F), Presence (P), and Constancy (Co) for each species

Species	S	A	C	F	P	Co
Usually found in upperstory:						
<i>Carya</i> spp.	5, 4, 3	4	1	93	100	5
<i>Quercus montana</i>	5, 4, 3	5	1	90	100	5
<i>Pinus virginiana</i>	5, 4, 3	4	1	89	100	5
<i>Quercus alba</i>	5, 4, 3	4	1	89	100	5
<i>Quercus velutina</i>	5, 4	3	1	83	100	5
<i>Robinia pseudo-acacia</i>	5, 4, 3	3	0	79	100	5
<i>Quercus marilandica</i>	5, 4	3	1	56	60	4
<i>Liriodendron tulipifera</i>	5, 4	1	0	30	80	2
<i>Pinus rigida</i>	5	2	0	25	60	2
<i>Pinus echinata</i>	5, 4	2	0	20	60	1
<i>Quercus borealis</i> var. <i>maxima</i>	5, 4	2	0	17	60	1
<i>Quercus stellata</i> Wang.	5, 4	1	0	17	40	1
<i>Quercus coccinea</i>	5, 4	1	0	17	40	1
Usually found in understory:						
<i>Nyssa sylvatica</i>	4, 5, 3	4	1	71	100	4
<i>Oxydendrum arborescens</i>	4, 3, 5	3	1	70	100	4
<i>Acer rubrum</i>	4, 5	1	0	38	100	2
<i>Diospyros virginiana</i>	4, 3	1	0	31	60	2
<i>Morus rubra</i>	4	1	0	17	40	1
<i>Cornus florida</i>	4, 3	1	0	20	20	1
Shrub layer:						
<i>Vaccinium vacillans</i>	2, 3	3	1	76	80	5
<i>Rhus toxicodendron</i>	2, 3	2	0	49	80	3
<i>Ceanothus americanus</i>	2	2	0	35	60	3
<i>Rubus</i> spp.	3	2	0	40	80	2
<i>Sassafras albidum</i>	3, 4, 2	1	0	23	60	2
<i>Rhus copallina</i>	3	1	0	13	40	1
<i>Kalmia latifolia</i>	3	1	0	11	40	1
<i>Hydrangea arborescens</i>	2	1	0	13	20	1
<i>Azalea nudiflora</i>	3	2	0	4	20	1
Woody vines:						
<i>Parthenocissus quinquefolia</i>	5, 1	2	0	27	40	1
<i>Vitis aestivalis</i> Michx.	4, 1	1	0	18	40	1
<i>Smilax rotundifolia</i>	2	1	0	16	40	1
Herbs:						
Leguminosae spp.	2	3	0	73	100	4
<i>Andropogon</i> spp.	2	2	0	63	100	4
<i>Panicum</i> spp.	2	2	0	62	100	4
<i>Solidago</i> spp.	2	2	0	59	100	4
<i>Hieracium venosum</i>	2	2	0	43	60	3
<i>Chrysopsis graminifolia</i> var. <i>asper</i>	2	2	0	39	60	3
<i>Houstonia tenuifolia</i>	2	2	0	36	60	3
<i>Chimaphila maculata</i>	2	2	0	35	80	2
<i>Tephrosia virginiana</i>	2	2	0	28	60	2
<i>Coreopsis major</i>	2	1	0	24	60	2
Gramineae spp.	2	1	0	23	60	1
Compositae spp.	2	1	0	27	40	1

TABLE 4 (Continued)

Species	S	A	C	F	P	Co
<i>Antennaria</i> spp.	2	2	0	19	40	1
<i>Pteridium aquilinum</i> , 2 var.	2	1	0	13	40	1
<i>Sericarpus asteroides</i>	2	1	0	13	40	1
<i>Tripsacum dactyloides</i> L.	2	1	0	20	20	1
<i>Steironema intermedium</i>	2	1	0	13	20	1

NOTE: Each of the following species occurred in only one station and therefore had a constance of six per cent and presence of twenty per cent: *Alnus rugosa*, *Amelanchier canadensis*, *Asclepias tuberosa*, *Aureolaria virginica* (L.), Farw., *Baptisia tinctoria*, *Castanea dentata*, *Cimicifuga racemosa*, *Dioscorea glauca*, *Euphorbia corollata*, *Fragaria virginiana*, *Fraxinus* sp., *Galium* sp., *Gaylussacia baccata*, *Gramineae* sp., *Heuchera americana* L., *Hypoxis hirsuta*, *Ilex opaca* Ait., *Juglans nigra*, *Plantago lanceolata*, *Polystichum acrostichoides*, *Potentilla* sp., *Rhododendron catawbiense*, *Schrankia angustata*, *Scleria triglomerata*, *Tecoma radicans*, *Viburnum prunifolium*, *Ulmus fulva*, *Prunus persica*.

dendron catawbiense, *Smilax rotundifolia*, and *Vaccinium corymbosum* var. *pallidum*. *Pieris* disappears along the east rim, being replaced by *Rhododendron catawbiense*. Here the thicket is tall and, in addition to the rhododendron and other species listed above, includes: *Leucothoe recurva*, *Gaylussacia baccata*, *Vaccinium vacillans*, and *Hamamelis virginiana*. Along the south rim the shrubs, chiefly huckleberries and laurel, are slightly less abundant. Herbs are scattered and of little importance except along the paths.

DISCUSSION

The Major Communities. Certain species are fairly abundant in all communities: namely, *Quercus montana*, *Nyssa sylvatica*, *Vaccinium vacillans*, *Orydendrum arborescens*, and *Robinia pseudo-acacia*. Other species are present in all communities but in lesser numbers. These are, in order of their decreasing abundance: *Pinus rigida*, *Kalmia latifolia*, *Carya* spp., *Andropogon scoparius*, *Leguminosae* spp., *Azalea nudiflora*, *Solidago* spp., *Quercus borealis* var. *maxima*, *Sassafras albidum*, *Panicum* spp., *Chimaphila maculata*, *Chrysopsis graminifolia*, *Pteridium aquilinum*, *Hieracium venosum*, *Houstonia tenuifolia*, and *Tephrosia virginiana*.

The four major communities are thus related by a number of species common to all. At the same time, they differ in a number of respects, which were used as a basis of distinction. First, a comparison of their frequency diagrams (fig. 2) indicates certain differences in homogeneity. The oak-hickory forest has far more species but fewer constants than either of the other communities. As indicated by the diagram, it is the most heterogeneous of the communities. The chestnut oak—heath, with the fewest species, is the most homogeneous community. This results partly from the almost total absence of an herb stratum. Although the chestnut oak—black pine forest has the largest number of species with average frequencies exceeding 80 per cent, its heterogeneity is exceeded only by that of the oak-hickory forest.

Differences are further emphasized by the restriction of certain species to single communities. *Parthenocissus quinquefolia* and *Vitis aestivalis* are so widely distributed in the oak-hickory forest and so rare outside of it that they may almost be considered as its indicator species. *Juglans nigra*, *Fraxinus* spp., and *Cercis canadensis* are also limited to this community; as are certain woody species which are exclusive to the ravines: namely, *Ulmus fulva*, *Morus rubra*, *Viburnum prunifolium*, *Prunus serotina*, *Chionanthus virginica*, *Viburnum acerifolium*, *Alnus rugosa*, and *Tecoma radicans*. A

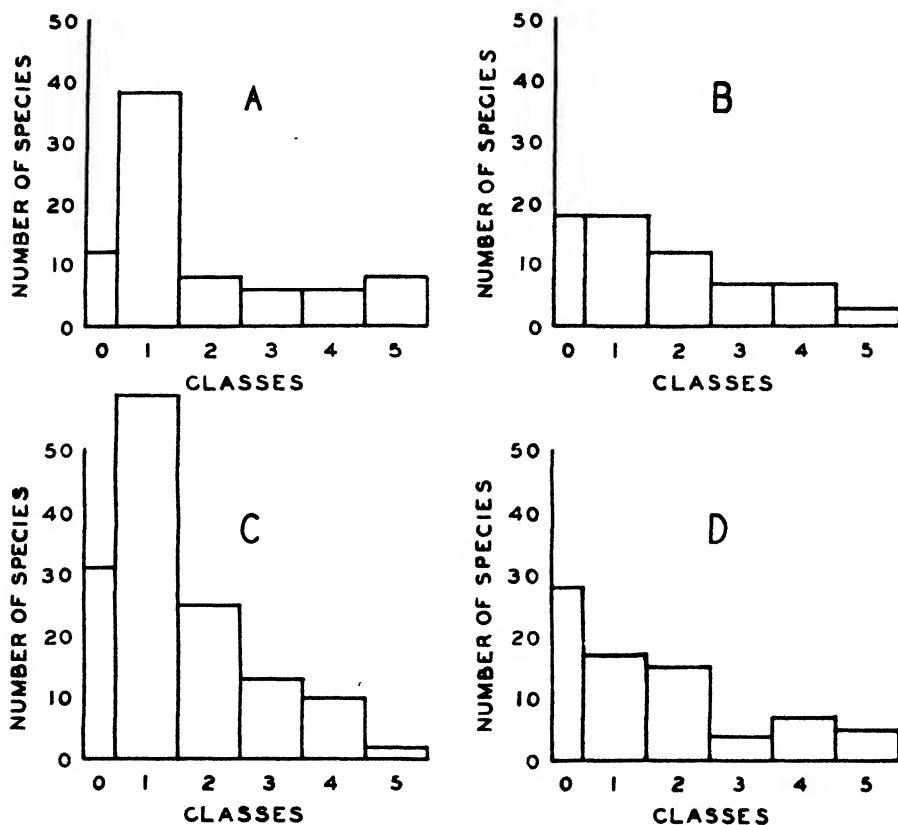


FIG. 2. Distribution of frequency classes in (A) chestnut oak—black pine, (B) chestnut oak—heath, (C) oak-hickory, and (D) mixed forest communities.

large number of mesophytic herbs, including most of the ferns, are limited to the oak-hickory forest. *Vaccinium corymbosum* var. *pallidum*, *Pieris floribunda*, and *Leucothoe recurva* are exclusive to the chestnut oak—heath, while *Rhododendron catawbiense*, *Gaultheria procumbens*, and *Quercus ilicifolia* are rare outside of it.

Although the chestnut oak—black pine and chestnut oak—heath communities appear to be superficially similar, careful study reveals certain funda-

mental differences, because of which the two were treated as separate entities. In addition to differences already stated, there is a great variation in the stratification. In the chestnut oak—black pine community the understory trees constitute the densest stratum, while transgressives are very important in the shrub layer; in the chestnut oak—heath the shrub stratum is decidedly the most important layer, few transgressives are present, and the seedlings are almost entirely of shrub species. In the chestnut oak—black pine community herbs are scattered but always present; in the chestnut oak—heath they are practically lacking except in paths and openings. In the oak-pine community black pine has essentially the same sociological values as chestnut oak and is generally and uniformly distributed throughout the forest; in the oak-heath, however, the pine largely occurs in small colonies, while oak is the general dominant. Furthermore, blackjack oak is a constant in the oak-pine community but is rare in the oak-heath.

Relationships to Mountain and Piedmont Communities. Although now all removed, the original forest of the Piedmont was hardwood with some pine (Oosting 1942). The principal trees in the virgin forest of Surry County were white, red, post, and chestnut oaks, maple, hickory, sourwood, tulip poplar, and white and shortleaf pine, and second growth of the same species now covers about 60 per cent of the county (Davis and Goldston 1937). Strangely, chestnut is not mentioned. At present there are very few shortleaf pine and still fewer white pine in the vicinity of, or on, Pilot Mountain. Virginia pine is abundant, characteristically occurring in young, dense stands as it does elsewhere in the upper Piedmont. Older forests near the mountain are similar to the mixed forest around the base of The Pilot.

Ashe (1922) described a black pine—chestnut oak—scarlet oak association as a forest type of the Appalachians found, in general, on north- and west-facing slopes in middle altitudes but, near its southern limits, confined to sandy or gravelly soils on northwest slopes at higher altitudes. This almost exactly describes the small area on Pilot Mountain in which scarlet oak is important. For lower crests Ashe lists Virginia pine, chestnut oak, table mountain pine, scrub oak [*Quercus ilicifolia* ?], tulip poplar, and white hickory. All these species except tulip poplar occur on the summit of The Pilot, with black pine in addition. Ashe assigns chestnut oak to "stone-loving associations" and states that chestnut oak consociations are especially found on soils derived from sandstone and shale. The scrub oak he assigns to small areas in the mountains of Virginia, West Virginia, and Maryland, and northward on shallow soils derived from sandstone and shale.

Cain (1930, 1931) describes certain communities of the Great Smoky Mountains, which he calls subelimax pine-heaths and which are very similar to the chestnut oak—heath on The Pilot. He attributes the heath balds of the

Smokies to a postclimax condition after landslide, windfall, or fire on sites in which ericads were abundant prior to burning. He also states that *Kalmia latifolia*, *Rhododendron catawbiense*, and species of *Vaccinium* are particularly resistant to fire. The associations he considered were on sandstone, sandstone conglomerate, quartzite, or slate, all of which produce inorganically acid soils. Except for altitude, these conditions are duplicated on Pilot Mountain and are evidently responsible for the chestnut oak—heath, which, near the base of The Knob, approaches the structure of a heath bald.

Thus the chestnut oak—black pine and chestnut oak—heath communities are evidently more closely related to the vegetation of the mountains to the west than they are to that of the Piedmont. Although certain species of the oak-hickory forest are similar to those of the climax forest of the Piedmont as given by Oosting (1942), the importance of chestnut oak and the presence of certain herbs more common to the mountains than to the Piedmont indicate that this community is likewise related to the vegetation of the mountains. The fact that, except for the mixed forest of the base, the vegetation on Pilot Mountain is more closely related to that of the Appalachians than to that of the surrounding Piedmont may be partly explained by the obvious effect of altitude and partly by the rock formation and soil found on the mountain. Quartzite is uncommon in the Piedmont, and the Hartsells soil is similar to sandstone soils that are found in the southern Appalachians (Davis and Goldston 1937).

Habitat Factors. As to habitat factors that may control the distribution of the communities on Pilot Mountain, it is difficult to generalize. The chestnut oak—heath and oak-hickory forest are usually present on steep slopes and flats; the chestnut oak—black pine community and mixed forest are found only on gently rounding slopes. Limitations in exposure and altitude have been pointed out in the descriptions of the communities. As to soils, the locations occupied by oak-hickory forest seem richest in humus. The north ravine down which the chestnut oak—heath extends and the ridges on either side comprise the single restricted area of Hanceville soil. The western half of the mountain seems more rocky than the eastern half, and the areas occupied by oak-hickory forest are, in general, less rocky than those above and below. The prevailing wind is from the southwest, and therefore the east- and north-facing slopes offer the most protected sites. Most of the rain clouds also come from the southwest, but, probably because of the contour of the mountain, there appears to be more precipitation on the northeast slopes than elsewhere. Thus a combination of factors restricts the most favorable sites to the northeast and north slopes east of Grindstone Ridge. The areas on the southeast and south that are occupied by oak-hickory forest appear to offer the next best conditions. Those occupied by the chestnut oak—black pine community are, in general, relatively xeric. The least

favorable of all sites are those around the base that are occupied by the mixed forest.

Disturbance. In addition to these continuously operating factors, a number of disturbances have influenced the extent and character of the vegetation. Rock slides locally destroyed the plants in their paths; the chestnut was removed by blight and fire; lumbering activities were extensive throughout the lower altitudes; and much of the area in the lower altitudes was formerly cleared. The influence of all these factors is, however, dwarfed by that of fire. The frequent burnings, which persisted until the building of the toll road, probably eliminated several species, while favoring the increase of those that were able to reproduce by sucker sprouts.

Succession and Modifying Factors. The oak-hickory forest is reproducing itself without any noticeable change, as is indicated by the frequent recurrence of its dominant species in the understory, transgressive, and seedling strata. It is therefore a climax community in which chestnut oak is the most important single species; tulip poplar forms societies of varying size; and northern red oak, white oak, several hickories, and black locust are important associates. In parts of the mixed forest that have not been recently disturbed the abundant hardwoods of the lesser strata indicate that this community is successional to the oak-hickory climax.

Generalizations on the dynamics of the chestnut oak—black pine community are complicated by the constant presence of pines in both understory and transgressive strata. The community is probably preclimax to the oak-hickory association, being controlled by the xeric conditions imposed by the thin, rocky soil. Although chestnut oak and blackjack oak may increase in importance, pine will probably remain abundant indefinitely because of the numerous openings in which it may grow to maturity. The extreme rockiness of the surface and the thin veneer of soil lessen the chances that the canopy may become closed. The small area in which scarlet oak is dominant is obviously a variant of the oak-hickory climax. Since pines are present in all strata, it has evidently not yet reached a climax condition. The chestnut oak—heath may be considered as a subclimax which is the result of repeated fires. Since seedlings of tree species are almost completely absent but shrubs are reproducing freely, the ericads will probably retain their present importance for some time.

A sawmill has recently been placed in the vicinity of The Pilot, and logs may be cut on the mountain itself. Such activities in the mixed forest should favor its retention in the present state. An increasing demand for lumber may cause the cutting of many of the trees in the oak-hickory forest, especially in lower altitudes. Whether such activities will result in an upward extension of the mixed forest remains to be seen. Because of their poor quality, it is doubtful that many trees in the chestnut oak—black pine com-

munity will be cut except for fuel. The unsatisfactory agricultural usefulness of the mountain has been amply demonstrated in the past. It is unlikely that any extensive clearing for cultivation will be attempted again, although the loam soils and the increased rainfall near the mountain will remain tempting to farmers.

The effects of all these possibilities are minor when compared to what might result if fire wardens relax their watch, a not improbable happening under present conditions. Should serious fires occur, chestnut oak, blackjack oak, red maple, and those shrubs which, like the trees named, come up from sprouts after fire, could increase in importance. Pines, however, might be temporarily increased since, under similar conditions in the Piedmont, pines have been found to appear and to grow so rapidly that a mixed forest resulted (Oosting 1943). Laurel and related ericads are now important in the moister sites within the chestnut oak—black pine community, and fire might cause the physiognomy here to become more like that of the chestnut oak—heath. The generally dry conditions of the area, however, are unfavorable to laurel, and the community, as a whole, would likely return to something similar to that of the present. Previous fires are said to have reduced the number of pines in areas now occupied by the chestnut oak—heath, and fire might conceivably bring this community nearer to a true heath bald. All species now present on the mountain have survived numerous fires and probably none would entirely disappear because of another burning.

SUMMARY

1. A phytosociological survey of the vegetation on Pilot Mountain was made during the summers of 1941 and 1942.

2. The Pilot is located in the southeastern corner of Surry County, North Carolina, and is the most southwestern outpost of the Sauratown Mountains. It rises nearly 1500 feet above the gently rolling plateau of the upper Piedmont to an altitude of 2413 feet. Quartzite caps the mountain. The soil is chiefly Hartsells stony fine sandy loam and is derived from the underlying quartzite, a rock formation that is uncommon in the Piedmont. Lumbering, cultivation, disease, and insects have affected the vegetation, but the greatest disturbing influence has been that of fire.

3. A statistical study was based on 158 sample areas, which were spaced altitudinally along "transects" ascending nine slopes and eight ravines. The data are summarized for each of the four major communities: chestnut oak—black pine, chestnut oak—heath, oak-hickory, and mixed forest.

4. The chestnut oak—black pine community covers the western half of the mountain and the higher southern slopes. *Quercus montana* and *Pinus rigida* are the dominant species. Important associates are *Quercus marilandica*, *Oxydendrum arboreum*, *Nyssa sylvatica*, *Vaccinium vacillans*,

Kalmia latifolia, and species of *Andropogon*. The community is probably preclimax to the oak-hickory association, being controlled by the xeric conditions imposed by the thin, rocky soil.

5. The chestnut oak—heath is found on the higher north and east-facing slopes. Locally its structure approaches that of a true heath bald. Chestnut oak and small colonies of pines are found in a widely scattered upperstory above a dense thicket in which ericads predominate. The community is very similar to the pine-heaths of the southern Appalachians and may be considered as a chestnut oak subclimax which is the result of repeated fires.

6. The mesophytic oak-hickory forest is a climax community found in the ravines and on the middle slopes of the eastern half of the mountain. *Quercus montana*, *Q. borealis* var. *maxima*, *Q. alba*, *Carya* spp., *Robinia pseudo-acacia*, *Liriodendron tulipifera*, *Vitis aestivalis*, *Parthenocissus quinquefolia* and a variety of herbs are important.

7. The mixed forest is found around the base of the eastern half of the mountain. *Quercus montana*, *Pinus virginiana*, *Q. alba*, *Q. velutina*, *Robinia pseudo-acacia*, *Nyssa sylvatica*, *Oxydendrum arboreum*, and *Q. marilandica* are the most important tree species. The mixed forest is a late successional community which, if left undisturbed, should rapidly approach the oak-hickory climax.

8. The mixed forest of the lower slopes is the only community definitely related to the vegetation of the upper Piedmont. All other communities show definite affinities to those of the southern Appalachians. This is probably related to similarities in soil and rock formation.

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SUBCLIMAX PRAIRIE¹

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The causes for the formation and persistence of the prairie peninsula which covers Iowa, southern Minnesota, and Wisconsin, and northern Missouri, Illinois, and Indiana, have formed the basis for much controversial speculation. The prairies from central Iowa eastward were classed as subclimax in the first edition of Weaver and Clements (43), but are shifted to climax in the second edition (1938), in which the entire peninsula is classed as a climax formation. This shift is in line with the stands of Shimek (32) and Transeau (38), but ignores much evidence that oak-hickory communities are capable of establishing and maintaining themselves on the most exposed sites and on most of the soils of Iowa, even though their rate of spread at many points may have seemed insignificantly slow.

Gleason (12) has summarized the taxonomic and earlier geological evidence for the establishment of the prairie peninsula in a post-glacial, xerothermic period of relatively recent date. Gleason cites invasion of the Illinois prairie, since grass fires have been controlled, at a rate which he considers proof of a forest climate at the present time. Aikman (1) found forest spreading in eastern Nebraska although he considered it to be a postclimax associates. Sears (30, 31) has published a number of papers on pollen analyses from the eastern end of the prairie peninsula indicating a gradual rise in temperature during post-Wisconsin time with one or more dry or xerothermic intervals, although pleistocene climate, except during glacial intervals, does not appear to have varied greatly from its present level. Simonson (33) has found buried soil profiles in Iowa which indicate that both soil-forming conditions and vegetation during the Sangamon inter-glacial period were similar to those that have prevailed during Peorian and recent times. Planosol profiles comparable to those currently present under grass (Putnam) or under forest (Marion), and gray-brown podzolic profiles comparable to the present Lindley (forest slopes), are found in Kansan till under 3-12 feet of Peorian loess. The distribution of these profiles indicates that the vegetation of Iowa during the Sangamon period differed from that at the time of settlement mainly in showing more forest in the western part of the State. Dissected valley slopes were covered by forest and the level till plain by prairie; with forest spreading onto the plain from the dissected areas.

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Lane (20) has shown by pollen analyses that prairies were prominent in Iowa in the interval between the Nebraskan and Kansan glaciations, but that coniferous forests both followed and preceded the various glacial periods. He notes that in neither the Aftonian nor the Sangamon inter-glacial periods did he find evidence of persistent hardwood forests. His findings thus do not support a recent origin for the prairie. Another paper by Lane (19) contains pollen analyses from a peat bog in Hancock County in north central Iowa which are significant as indicators of climatic conditions during the last few thousand years. Observations on a 15-foot peat section showed that at least the immediately surrounding areas of this late Wisconsin (Mankato) drift section have been covered successively by (a) spruce, (b) mixed coniferous forest, (c) hardwood forest or savanna, and (d) grass, since the recession of the Wisconsin lobe which covered north central Iowa. Grass pollen first became prominent (14 per cent) in the 11th foot at the time of the shift from coniferous to deciduous forest species, and was dominant (60 per cent) in the 7th foot of the deposit. Weed pollens suggestive of recently bared areas, possibly of intermittent drying of the lake, accompanied the disappearance of the oak in the 8th foot, and reappeared in the 5th, 4th, and 3rd feet. There seems to be no doubt that all of the peat studied had been formed since the recession of the Wisconsin lobe some 20,000 years ago. We may assume that peat accumulated slowly at first in the deeper lake and that the lower 6 feet, in which various tree pollens were dominant, cover more than half, possibly more than two-thirds of post-Wisconsin time. We may assume also that with the filling of the lake and lowering of the outlet, peat deposition was accelerated until it may have approached a rate of one foot in 100 or 200 years. Lane's bog lay within a belt of low morainal hills which should have been better adapted to forest than the glacial till plain. We cannot assume therefore without further analyses that all or even most of Iowa has been forested in post-Wisconsin time. His data, however, seem to show clearly that the climate of Iowa has become warmer and drier during this period, and that the vegetation of the state has been subjected to unusual drought stress on two occasions, the first probably 5,000 to 8,000 years ago and the last possibly as recent as 500 to 1,000 years.

Lane's analyses, taken together, indicate that prairies have been prominent, if not dominant, in Iowa since the beginning of the pleistocene or glacial age, and he interprets them as supporting a climax classification for the prairie. The grassland community covered from 80 to 90 per cent of the state of Iowa at the time of white settlement, and was so thoroughly established on all but the rougher lands of the southern and eastern counties as to seem to justify a climax ranking. Transeau (38) has attempted to establish a tongue of prairie climate over the peninsula which would make it a true or climatic climax. Others (6, 7, 12) feel that the prairie peninsula,

including most of Iowa, is a relict of glacial disturbances maintained by soil factors, past xerothermic periods, and fires, and is therefore subclimax (to forest) or postclimax (to climax prairie) or disclimax (maintained by fire and soil factors), but in any event not true climax under present conditions.

Our justification for adding to the already voluminous literature of the prairie peninsula is based upon: (a) additional evidence of the recent rapid and general advance of forests in the critical western counties of Iowa; (b) observations upon the effects of the 1930-1939 dry cycle on Iowa forests; (c) soil studies which bear upon the problem of the advance of the forest; and (d) evidence for previously unrecognized soil factors retarding afforestation of the prairies of Iowa. While our observations are principally on Iowa, as the exposed, western base of the prairie peninsula, the discussion is extended to include similar grasslands wherever found. To forestall possible disagreements over terminology, we do not include soil factors, with their continuous changes from weathering and reaction, in our definition of true or climatic climax.

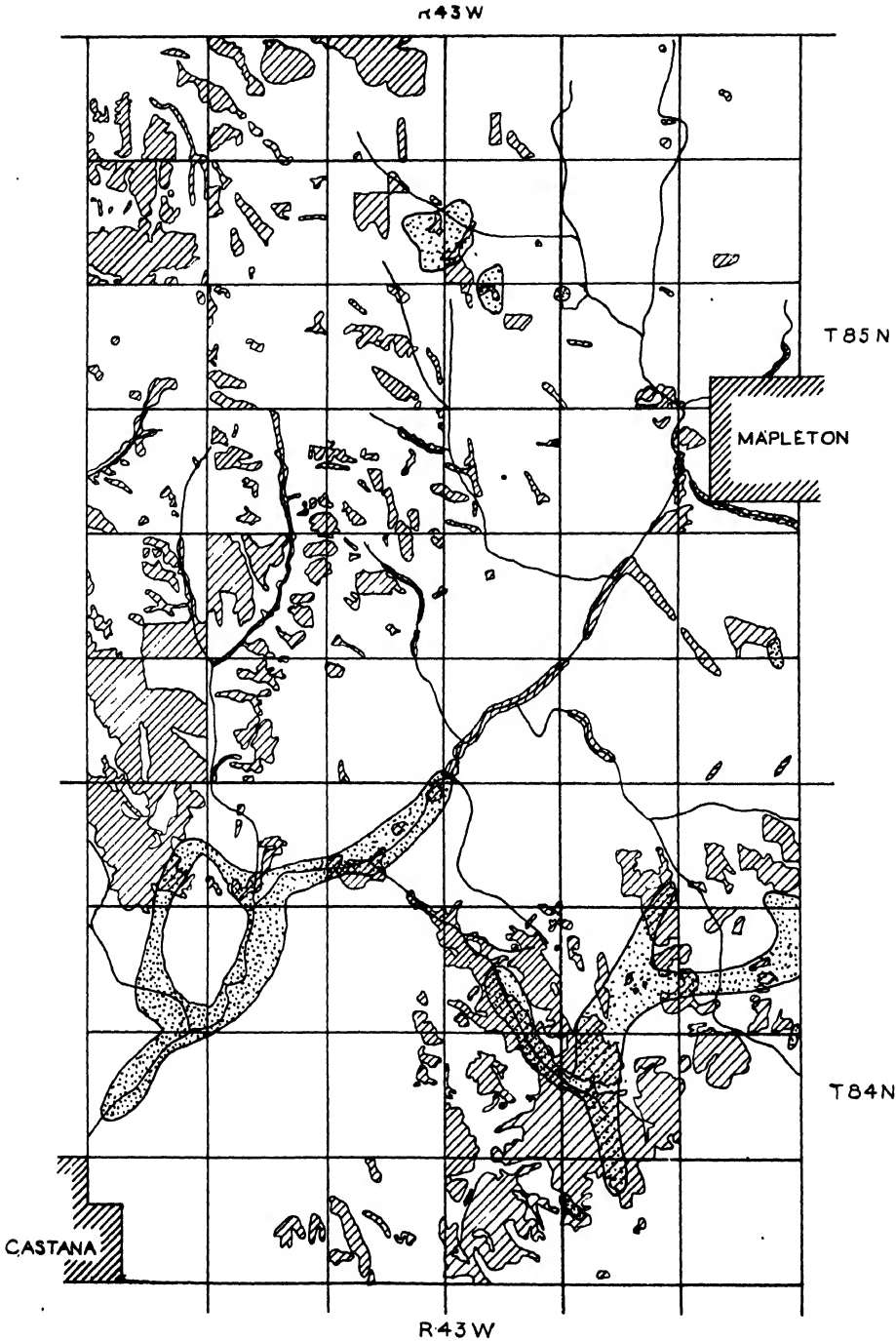
RECENT AFFORESTATION IN IOWA

A plant community which occupies more than 90 per cent of an area would normally be assumed to be the climax formation, and notes of the original surveyors show that many west central Iowa counties were almost treeless. If we assume a recent climatic shift, however, and the evidence for such a shift is unmistakable, the climax formation would be identified by its current invasion and ecesis rather than its distribution. On this basis, the loess hills of western Iowa, surprisingly, show striking evidence of recent rapid invasion by forest. Harrison, Monona, and Woodbury counties, on the Missouri river in central western Iowa, lie at the western edge and near the most exposed and the driest portion of the prairie peninsula. Harrison county vegetation was used by Shimek (32) to support his thesis of climax prairie in Iowa, yet 30 years later *Quercus macrocarpa* is spreading so rapidly on the less intensively farmed lands of the county as to constitute a serious economic problem.

Direct evidence of current afforestation in these critical western Iowa counties is furnished by two maps contrasted in figure 1. The distribution of the original forest, as mapped section by section in 1853 by the original public land surveyors, is shown along with the present forest cover mapped from aerial photographs taken for the Agricultural Adjustment Administra-

Explanation of figure 1

FIG. 1. Forested areas in Maple (85 N.) and a part of Center (84 N.) Townships in Monona County, Iowa. Dotted areas show closed forest of 1853, before settlement, and cross-hatched areas represent present forest distribution. Compare figure 2 which shows some of the west central portion of this area.



tion in 1940. The maps cover most of two townships located in the loess hills of Monona county just east of the Missouri river bottoms. The soils of this area are of the Knox-Monona association. No podzolized soil profiles have been mapped in extreme western Iowa although small areas of forest soils recently have been discovered about 30-50 miles southeast of the area shown in figure 1. The lack of forest podzolization in this region indicates that the establishment of forest areas in this "prairie climax" was recent in time, probably within the last 1000 years, as well as limited in extent at the time of settlement of the region. Buried soil profiles in this region (33) show evi-

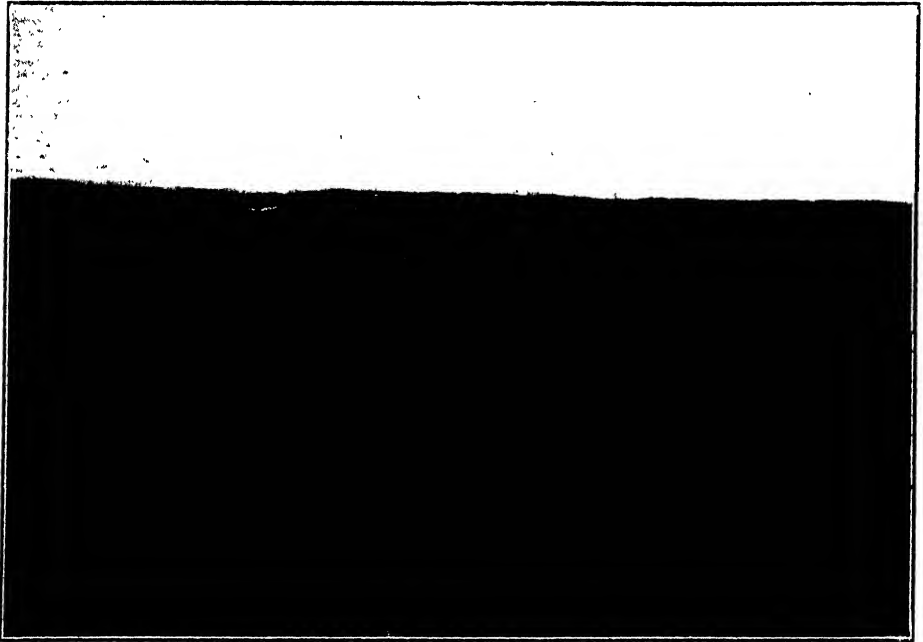


FIG. 2. Aerial photograph of the southwest corner of Maple Township showing 50 per cent or more of this original prairie covered by forest and woodland pasture. In 1853 "A few small groves—with a few scattering burr oak comprised the timber of the township."

dence, however, of the presence of considerable forest during the Sangamon interglacial period.

An aerial photograph of a portion of the area in figure 1 is shown in figure 2. This region was surveyed in 1853 as prairie with scattering trees or clumps of trees. The present forest cover has spread naturally, most of it in the last 50 years. Invasion has been most rapid, of course, in protected sites, but has resulted in the afforestation of exposed as well as protected slopes and of rounded ridge tops. The narrow, hogback ridges, which were once classed in a separate soil series, resist invasion even on northeast exposures and when partially shaded by well developed forest. Local soil factors would

appear to be involved. Most of the trees shown in the figure are *Quercus macrocarpa*, and only a few of them are more than 50 years old. Brush lands are in part reproduction from stumps and in part new invasion which is still proceeding. Most of this timber is, as shown in figures 3 and 4, rather scrubby

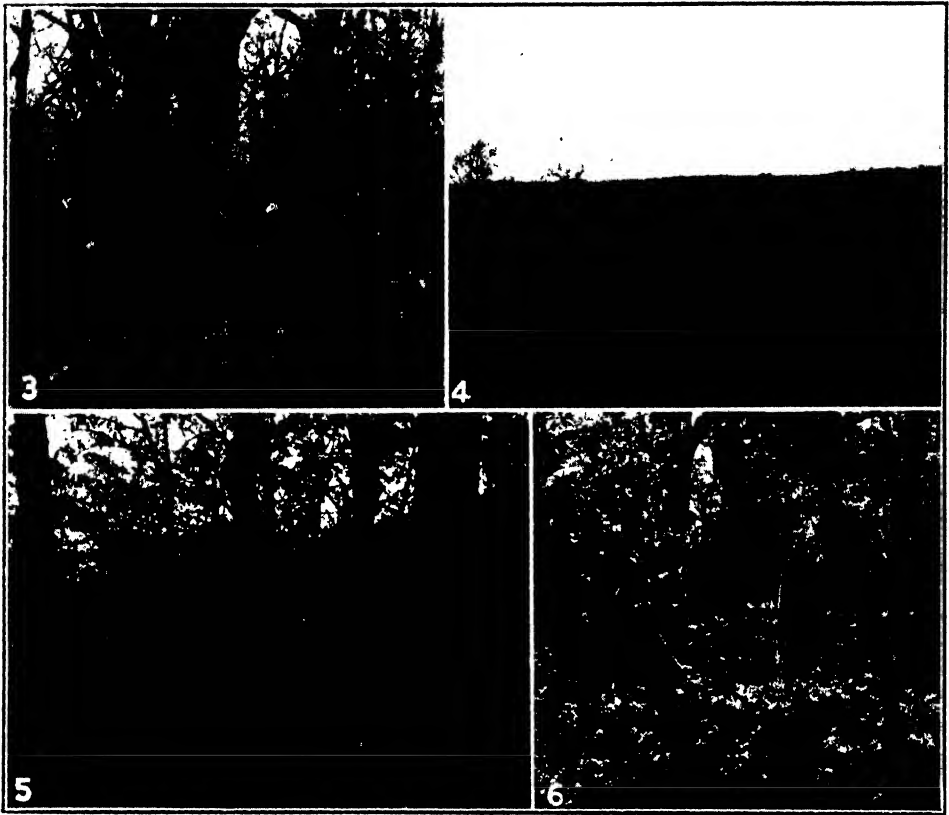


FIG. 3. A low-branched, 78-year old seed tree of *Quercus macrocarpa* surrounded by 40-50 year old trees which have formed a closed canopy with an understory of *Cornus*. Fully exposed ridge top in the center of section 31, Maple Township. FIG. 4. *Quercus borealis* and *Q. macrocarpa*, closed forest and cutover pasture. Looking southeast across section 10, township 86 north, range 43 west; Woodbury County just north of Maple Township in Monona County (cf. Fig. 1). FIG. 5. *Quercus borealis* closed forest with typical forest undergrowth on southwest slope in section 15 of township 86 N. Oldest trees about 50 years. FIG. 6. Seedlings of *Ulmus americana* and sprouts of *Quercus macrocarpa* on hilltop land in section 15, Maple Township. The elm apparently seeded into over-grazed pasture early in the 1930-39 dry cycle.

burr oak. The stands are closing or closed, however, until prairie species have been largely excluded and other forest species are now appearing. *Quercus borealis* (fig. 5) is capable of maintaining full stands on the most exposed sites, and is spreading into the burr oak, along with *Carya cordiformis*, as

seed trees develop. *Ulmus americana* is common, invading disturbed areas rapidly (fig. 6) and persisting as dominant trees even on the most exposed areas. *Tilia americana* grows vigorously on protected north slopes. *Juglans nigra*, *Gymnocladus dioica*, *Celtis occidentalis*, and others are found as scattered individuals, typically in more protected locations. *Fraxinus lanceolata* is moderately common, and the usual willows, maples and elms occupy the stream banks and younger flood plains.

The large areas of pure stands of burr oak, the prominence of *Cornus* rather than *Ostrya* as an understory, and the absence of old trees or stumps all testify to the recent establishment of these woodlands. The frequency with which the larger trees on many sites showed ring counts of 45 to 50 years suggests that a general climatic or economic disturbance, such as drought and over-grazing or abandonment of marginal farms, during the 1890's, may have accelerated the current invasion. Acceleration of invasion of grasslands by grazing is a common observation in the West and Southwest (9, 21). If forest was already invading slowly and the new community is able to develop vigorous stands on exposed sites, climax relationships are not involved, and the effect of the disturbance is considered to have been accelerative only.

Adequate evidence that the current trends antedate the disturbances which have hastened them is contained in notes made by the original surveyors and preserved in the State House at Des Moines. Excerpts from these notes for several townships in Monona and Woodbury counties, all of which were mapped in 1853, follow:

Twn. 83 N., R. 43 W., 5th P.M. David J. Sales, Deputy Surveyor. "Young timber is evidently extending into the prairie, and in many places there is a growth of young burr oaks, lind and hickory on high ground where there is no water course. We found no inhabitants or improvements in this Township."

Twn. 84 N., R. 43 W., 5th P.M. (cf. fig. 1), David J. Sales, Deputy Surveyor. "This Township (excepting the river bottom) is generally rolling, with some young timber scattered over it, generally burr oak and lind and numerous small thickets of young burr oak, lind and hazel which are evidently spreading in despite the fires which burn off the grass."

Twn. 85 N., R. 43 W., 5th P.M. (cf. figs. 1-3, 6, 13 and 14), John W. Ross, Deputy Surveyor. "The greater proportion of the Township is high rolling prairie. Soil 3rd rate. . . . A few small groves of timber principally maple lynn and elm with a few scattering burr oak comprise the timber of the Township."

Twn. 88 N., R. 43 W., 5th P.M., John W. Ross, Deputy Surveyor. "The Soil of which is poor 3rd rate. In the prairie are burr oak scattered all over."

From these notes and others not quoted we get the impression that the surveyors mapped as forest all tree-covered areas with a closed canopy, from

which the prairie grasses had been excluded either by trees or by trees and associated shrubs. The areas mapped as prairie thus probably consisted of both true prairie and burr oak savanna. In reading through notes for individual sections, quarter corners and section corners in areas mapped and spoken of as prairie were often witnessed by burr oak trees. These witness trees were frequently 200 to 300 feet from the section corners, indicating an open savanna, while their descriptions indicate young trees. In these localities at the present time there are areas of apparently lightly grazed original prairie in which are a few scattered burr oak trees. These areas of savanna are probably very much like areas found at the time of the survey.

In the 80 years since the area was first settled most of the original timber has been cut or cleared, and it is now difficult to locate any of the forest plotted in 1853. On the other hand the forest has invaded so generally and in such a wide variety of new sites as to leave little doubt that the climate at this extreme western end of the prairie peninsula is fully capable of supporting an oak-hickory climax. Invasion has followed land use patterns rather than topography, and recently forested spots are on rough, poor, and inaccessible land rather than in protected stream valleys. Much of the heaviest invasion appears to have been on foreclosed lands which have lain fallow or only partially utilized. Both new invasion and older stands may be found on hilltops and on south and west slopes (figs. 2-6), indicating that these forests require no protection from wind and sun. It should be noted, however, in connection with later discussions that these soils are formed from a deep, well-aerated loess subject to more rapid erosion than is characteristic of most of the prairie peninsula; also that surface and internal drainage are excellent and the soil nitrogen content low.

FOREST INVASION IN CENTRAL IOWA

Invasion in western Iowa has been favored by less intensive land utilization, by the rather general distribution of seed trees, and, as we shall note later, by soil conditions suitable for forest growth. On the Wisconsin drift soils of central and north central Iowa conditions have been less favorable for forest. Planted trees grow well throughout the region, however, and seedlings become established readily wherever the sod has been broken up (figs. 7, 8). In contrast an undisturbed *Poa pratensis* sod may delay invasion for years (fig. 9), and the rank growth of the original prairie was undoubtedly an inhospitable site for forest seedlings. Under these conditions primary invasion occurred along the streams where erosion had broken up the sod (figs. 11, 12, 21), and invasion of the till plain occurred in the usual shrub ecotone rather than by the widely scattered seed trees which have been the basis of the rapid afforestation in western Iowa. Current invasion is limited by intensive land utilization, but adequate evidence of moderately rapid

presettlement invasion of the prairie is shown by surveyors' notes and soils maps.

The coarser, lighter-colored prairie soils of the Wisconsin drift area in Iowa are mapped as Clarion, the finer-textured, black soils of the poorly drained swales as Webster. Forest on eroded valley slopes has formed the

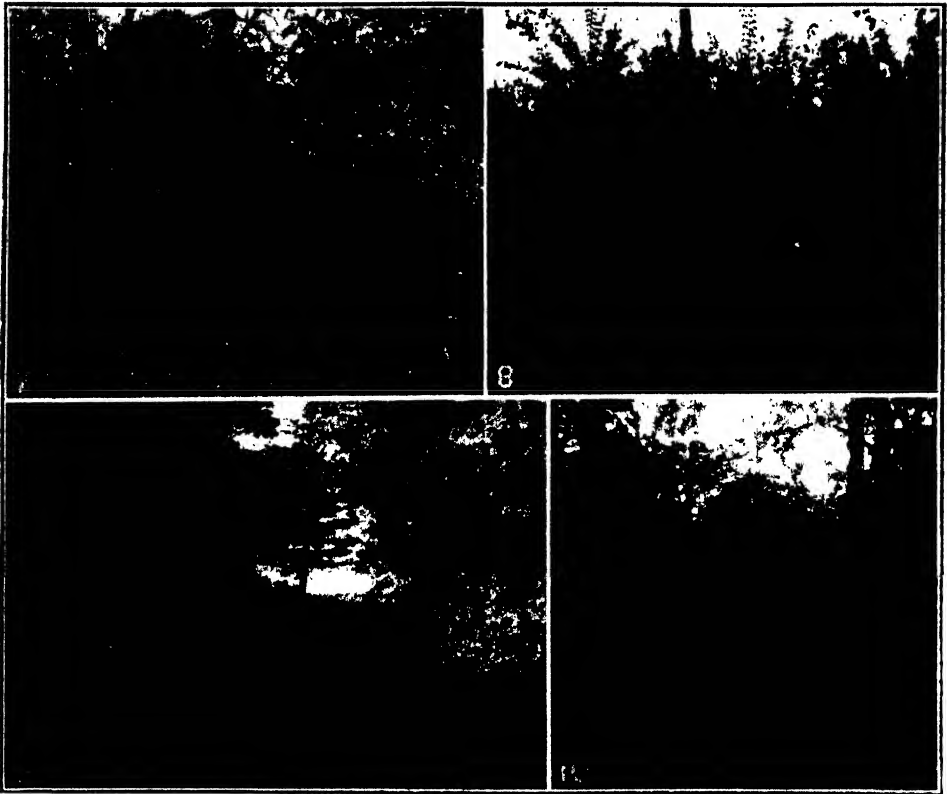


FIG. 7. Natural reproduction of *Juglans nigra*, *Acer saccharum*, *A. saccharinum*, *A. negundo*, *Fraxinus lanceolata*, *Celtis occidentalis*, and *Ulmus americana* in an abandoned kitchen garden. Prairie hilltop site; Clarion loam soil; Story County in central Iowa. FIG. 8. *Ulmus americana* seedlings on a road bank bared in grading operations three years previously. South exposure; no seepage from back. FIG. 9. The lawn of the same farmstead shown in figure 7. Undisturbed *Poa pratensis* sod has prevented the establishment of seedlings on this portion of the plot. FIG. 10. Second growth oak-hickory forest (*Quercus alba*-*Carya ovata*) on Wisconsin till (Ames soil type); Story County, Iowa.

Lindley, and on the till plain the Ames soils. Ames soils are formed from the same parent material as the Clarion, but under the more rapid podzolizing influence of the forest they have developed a gray, leached A₂- and a plastic B-horizon, to form inferior agricultural lands known as "oak lands" (figs. 10-12, 21).

Estimates of the time necessary for the formation of a planosol like the Ames or a gray-brown podzolic soil like Lindley are not available. Minimum estimates for the formation of podzols under spruce forests at more northerly latitudes are from 1000 to 1500 years (5). Under the climatic conditions of the western prairies and with a highly calcareous glacial till as parent material, a much longer period may be required for formation of mature soil profiles. The flat tops of several low Indian mounds on a forested divide near the Des Moines river in Boone county, Iowa, showed no visible evidence of

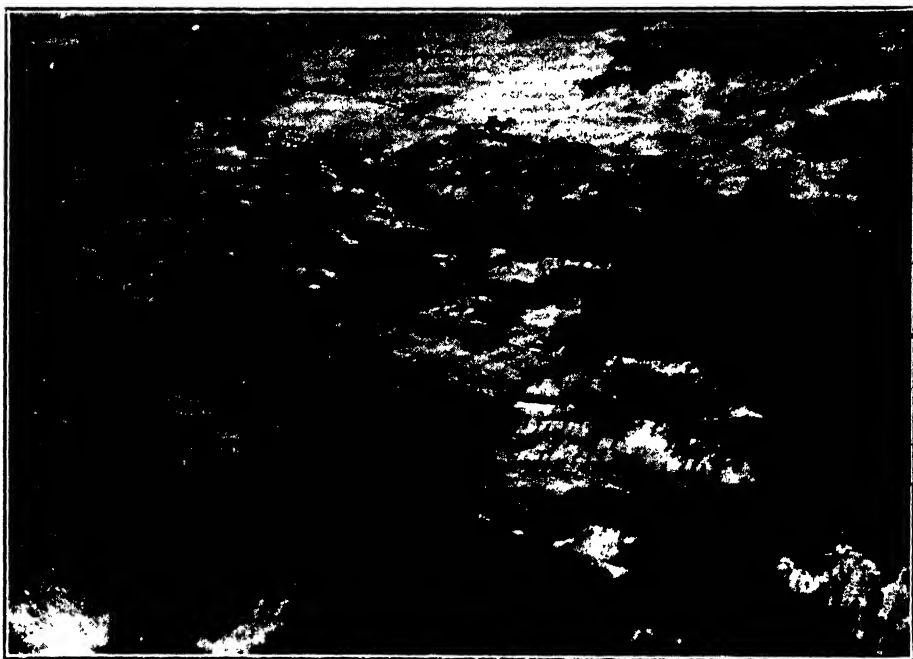


FIG. 11. Erosion and forest invasion along the Des Moines River, Boone County, Iowa. The oak-hickory forest has advanced along the deep gullies cut back from the glacial stream valley, and then spread over the prairies of the nearly level till plain. Scattered oaks in pastures and farmyards at the left and back are evidence that most of the area shown was originally covered with forest. (Photo by P. H. Carr.)

the development of a leached A_2 -horizon, nor could any accumulation of clay to form a B-horizon be detected. These mounds are classed as woodland culture by Dr. C. R. Keyes, State Archaeologist, and are variously estimated to be from 1000 to 5000 years old. Undisturbed soils near the mounds showed a typical Ames profile with a heavy, plastic B-horizon. From this and other evidence it seems probable that from 1000 to 2000 years have been required in Iowa to produce detectable soil changes under forest, and that the fully developed Ames profile indicates a forest cover for considerably more than 2000 years.

Close examination of the soils of oak-hickory forests on the Wisconsin till plain shows that, with similar topography and drift material: (a) the outer border of the Ames soil is sharply demarcated; (b) there are often spots or bands of partially podzolized or degraded Clarion soil between the Ames and the Clarion; and (c) beyond the degraded Clarion an oak-hickory forest existed on typical Clarion prairie soil showing no visible evidences of podzolization or long occupancy by forest. The sharp outer border of the Ames probably indicates a long pause in either invasion or retreat, for had conditions been uniformly favorable or unfavorable for forest the Ames would blend gradually with the Clarion. The presence of forest beyond the areas of Ames soil is undisputable evidence of a more recent invasion, probably one taking place in two steps, the first of which occurred long enough ago to permit partial podzolization of the invaded Clarion, and the second so recent as to leave no visible change upon the soil.

The distribution of Ames and Lindley soils bordering typical prairie streams in Story county, Iowa, along with the prairie-forest border mapped in 1847, are shown in figure 12 (*cf.* fig. 21). This map shows several items of interest: (a) The forest mapped along these prairie streams in 1847 exceeded the forest soils by more than four to one—clear cut evidence of a presettlement forest invasion so recent that no detectable soil profile changes had occurred. (b) The forest was advancing more rapidly along the streams than onto the till plain. (c) Eighty per cent of the forest soils are east of the streams and all of the Ames (till plain) soil is protected on the northwest by the streams, by steep banks or by marshes. In contrast, 40 per cent of the original forest lay west of the stream, most of it fully open to the northwest. Gleason (12) gives planimeter measurements of several Iowa maps showing that 70–80 per cent of the forest lay to the east of streams or lakes. He attributed this distribution to the firebreak action of the water. Fuller (10) records the same distribution of forest soils in LaSalle county, Illinois, and points out that low banked streams, or east-west streams, which would not have acted as firebreaks, showed no development of forest soils. It seems evident, however, that if fire was the major factor causing the unequal distribution in figure 12, the more recently established forests would have been affected as well as the older. In southern Iowa, where fires should have been equally prevalent, forest soils have been formed on slopes west and southwest of the streams—fully exposed to fire but protected from the drying effects of sun and wind. In addition to fire, this unequal distribution of forest soils on the Wisconsin drift may have been associated with the windbreak and afternoon shade protection afforded seedlings by the main forest body to the west, and by the fact that soils on the east sides of streams in Iowa and Illinois (34) often contain windblown sand and are somewhat lighter in texture.

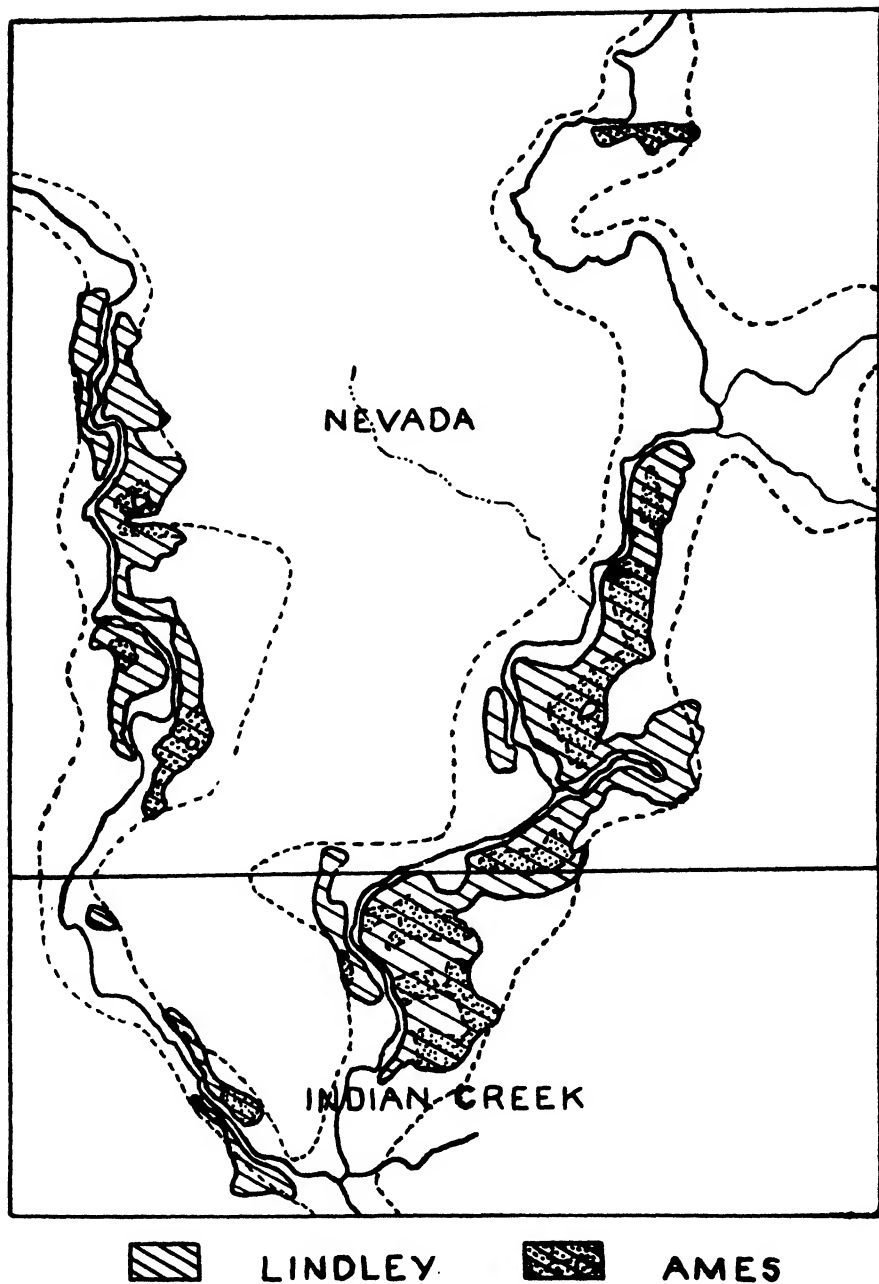


FIG. 12. Forests and forest soils in two Story County townships. In 1847 the streams were bordered by forest as shown by dotted line. Older forest had developed Lindley soils on valley slopes and Ames on the till plain. More than three-fourths of the forest had been established so recently that the original prairie soils were unaffected (*cf.* fig. 21).

Irrespective of the factors affecting distribution, the evidence seems to require the conclusion that forest has increased 300 per cent or more along these prairie streams in the last few hundred years, but that this advance was preceded by a considerably longer period during which little or no advance occurred. Abundant evidence of this recent forest advance is found along the Des Moines river and generally throughout the central and north-

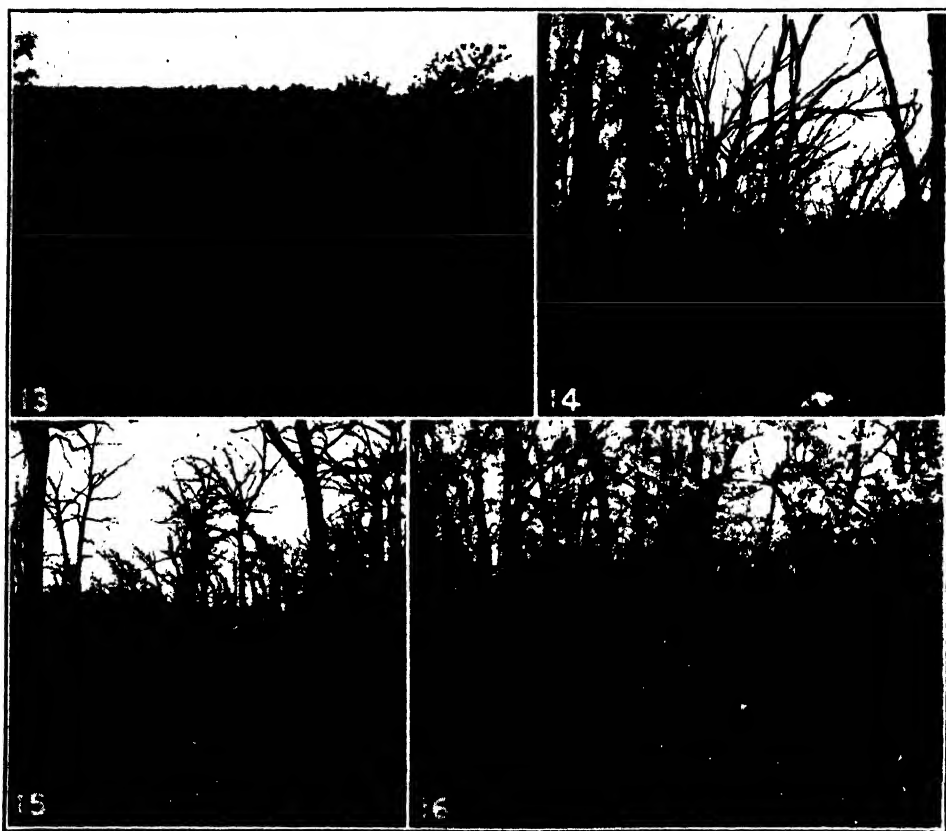


FIG. 13. Young trees of *Quercus macrocarpa* in exposed and ungrazed prairie showing no damage from drought. Monona County, May 1937. FIG. 14. Dominant trees of *Ulmus americana* dead and *Quercus macrocarpa* injured in protected pasture. Monona County, May 1937. (cf. figs. 3-6). FIG. 15. *Quercus macrocarpa* in over-grazed pasture with southwest exposure dead or killed back to main limbs. Woodbury County, May 1937. FIG. 16. No injury in mixed hardwood reproduction. One hundred yards east of area shown in figure 15 and same exposure.

eastern part of the state. On deep loess soils in the northeast corner of Iowa entire townships of prairie soil were covered by recently established forest. It is noteworthy, however, in connection with soil factors to be discussed later, that no comparable recent advance has occurred on the older soils of

the Kansan drift and associated loess in south central and southeast Iowa, an area which contained much of the state's original forest cover.

FOREST SURVIVAL DURING THE 1930-1939 DROUGHT

The years from 1930 to 1939 covered one of the most severe and protracted dry periods in the recorded history of the Mississippi valley. If the normal climate of Iowa is that of a grassland climax, forests should have suffered severely during this dry cycle. Paradoxically, although hundreds of thousands of adapted trees on suitable or even protected sites were killed or very severely damaged, *forests* were not visibly affected. Unpastured savanna of *Quercus macrocarpa* in original prairie showed no injury on a severely exposed site in Maple township, Monona county (fig. 13), but heavily pastured burr oak a few miles north in Woodbury county was killed or severely injured (fig. 15). *Ulmus americana* was killed and burr oak injured on a moderately pastured north slope (fig. 14), while no signs of injury were evident in unpastured reproduction on the south slope of the same hill (fig. 6). In general, pasture fences marked the difference between serious injury to complete killing and no injury whatever (figs. 15, 16). In many of the pastures no perennial grasses could be found in May 1937. Conditions were ideal for rapid invasion by tree seedlings, particularly where the farmers had been forced to dispose of stock for lack of feed, but older trees were injured in spite of reduced competition. The only factor that could be associated consistently with drought injury was trampling of the soil. Trampling would have reduced rainfall penetration, but evidence to be presented later suggests that reduced aeration was the more important factor. *Quercus macrocarpa* is deep-rooted on these loess soils (fig. 23). Trampling, particularly heavy stocking of the finer-textured soils in early spring, would reduce gas exchange rates and so limit depth of root penetration, rate of absorbing root production and efficiency of roots present.

The recent drought seems thus to have furnished a clue to forest invasion and survival as well as evidence that undisturbed forest formations are able to withstand one of the severest droughts on record, at the dry western edge of the prairie peninsula. This lack of drought injury, coupled with presettlement and continuing forest invasion, indicates that the current climate of western Iowa is not too xeric to support an oak-hickory climax, and thus relegates the grasslands of the prairie peninsula to a subclimax ranking.

FACTORS FAVORING SUBCLIMAX PRAIRIE

The establishment of oak-hickory forest as the climax formation of Iowa leaves unexplained the presence of tall grass or true prairie as the dominant vegetation, covering 80 per cent or more of the state at the time of settle-

ment. Past attempts at explaining prairies have stressed climate, biologic factors, fire and soil factors. Undoubtedly all of these are concerned in varying degree in the persistence of the prairie peninsula.

Climatic Factors. Although our observations have shown oak-hickory forest capable of spreading and maintaining itself on the most exposed sites of western Iowa and in some of the driest years of record, the climate of this region is clearly borderline between the forest and the grassland climax. The rainfall of about 30 inches falls predominantly during the growing season. The amount and rate of precipitation in individual storms are high enough, however, to permit the subsoil wetting necessary for a deciduous forest, and moist soil from the surface to the water table at some part of the year is characteristic if not universal. Such rainfall distribution, while favorable to grass, is not unfavorable to forest.

Rainfall-evaporation ratios have been used as one of the better indices of climate as it affects vegetation. Unfortunately very few evaporation measurements are available for the construction of such ratios. Weather Bureau records of evaporation for the seven months April to November are available for the last ten years at Ames in central Iowa, and for five years at Clarinda in the southwestern and Cherokee in the northwestern part of the state. The seven months rainfall-evaporation ratio at Ames for the years 1933-1942 was 0.50. The average for five dry years was 0.35 and for five years with normal or excessive rainfall, 0.65. For the nearly normal five-year period 1938-1942, the ratio of the *seven months* evaporation to the *twelve months* rainfall was 0.72 at Ames, 0.70 at Cherokee and 0.64 at Clarinda. While winter evaporation is low, available estimates indicate that its inclusion would have lowered these ratios by 5-10 per cent. It seems probable, therefore, that the current rainfall-evaporation ratio in western Iowa is about 0.60. In contrast, Transeau (37) set 1.00 as the ratio for continuous forest and 0.60 as the border between prairie and short-grass plains. His ratios were based on data of a single year and would seem to be too high. An annual evaporation rate that is 170 per cent of the precipitation, however, cannot be considered ideal for forest, and is an index of the stress against which forest invasion is occurring.

Evidences of the recent dry or warm-dry periods stressed by Gleason (12) are unmistakable in Lane's pollen analyses (19) and in the Wisconsin drift, forest soil-forest distributions. These data give a picture of the oak-hickory forest only recently resuming its advance after a long period of stagnation. The presence of degraded or partially podzolized Clarion soils indicates that recent invasion has occurred in two waves separated by a period relatively unfavorable for forest. A picture of the time involved in these sequences can be obtained from Lane's Hancock County peat (19).

Assuming that the weed stages represent dry periods when the lake was partially dried up, that the rate of filling with peat increased gradually from zero at the bottom to 1 foot in 200 years for the upper foot, and that peat deposition occurred over a period of 20,000 years, the first dry period, represented by a sharp drop in oak and increase of grass pollen in the 7th foot of the deposit, would have occurred at a minimum of about 3500 years ago and at the maximum possibly 8000 years ago. The more recent weed stage and dry cycle, shown from the 5th to the 3rd foot, would have occurred approximately 1000 years ago with a minimum estimate of 400 and a maximum of 2000 years. The estimates for the first dry cycle correspond with those of 2000 to 6000 B.C. given by Antevs (2, 3), and with the estimates of Brooks (4), based on many records indicative of a general dry cycle over at least the mid-latitudes of the northern hemisphere. The more recent general dry period is estimated by Brooks to have occurred between about 800 and 1600 years ago and to have ended about 1100 A.D.

As the climate of late-glacial and post-glacial time gradually became warmer, the spruce forest that followed the ice was replaced by oak-hickory forest on the coarser-textured soils. Although evidence is lacking, it is possible that the flat, poorly aerated till plain (fig. 21) went directly from spruce to grass. The first dry period may be assumed to have driven the forest back to the borders of the present fully developed forest soils; Ames on Wisconsin till, Clinton and Marion on Peorian loess overlying Kansan till, etc. This scheme allows 6000 to 8000 years for the formation of the Ames profile, and assumes that the interval between the two drier periods was still too dry for forest invasion until toward the end, when the advances represented by scattered strips of degraded Clarion were made. Six thousand years is probably above the minimum time for forest soil profile formation in Iowa, but there is no upper limit, and we feel that 2000 years is below the minimum under the conditions which have existed. No intervening period fits with the climatological data available from many sources.

We thus arrive at the conclusion that, except for a short period some 2000 or 3000 years ago, grass was the climax formation of Iowa from 3000 or 6000 B.C. to 1000 or 1200 A.D., and that the present forest climate has had only a few hundred years in which to affect the vegetation of the area. Lest our outline seem too assumptious, may we repeat that soil profile data, all available fossil pollen analyses, and the best estimates of past global climatic shifts are in agreement in supporting its essential points.

Biologic Factors. Even with a longer period than has been available for forest invasion, the difficulties of seed distribution and seedling establishment under grass competition could account for the lack of forests in central and western Iowa. Direct invasion without a shrub ecotone, such as is re-

quired for rapid spread of the forest, is complicated by the fact that few forest species are fitted to compete with a prairie vegetation. Invading tree seedlings must develop a long tap root the first growing season if they are to get below the zone of heavy moisture use by grass and survive summer droughts. They must also make enough shoot growth to emerge from the dense lower layer of the prairie and make food for continued growth, and they must be capable of withstanding relatively long periods of drought when the soil moisture level is at the wilting point and the air temperatures within the drying grass, which affords little shade but effectively stops cooling air currents, may be above the death point of many plants. The first two characteristics are met with only in the large-seeded species, and when one considers periodicity of seed years and the great abundance of rodents in the prairie, the difficulties of invasion and ecesis are evident. Most of the species of oak seedlings also require some shading and moderate temperatures (17). In southern Iowa reproduction of cut-over oak stands in almost exclusively from sprouts, and seedling reproduction is successful only when small openings are made in unpastured and unburned forest. In central Iowa oak reproduction in non-forest areas is so rare that the presence of oak trees in a farm lot or fence row is taken as evidence of original timber (fig. 11). When these growth requirements are matched against the characteristics of available species, *Quercus macrocarpa* is the only one obviously fitted for invasion, but its high seed weight tends to limit dispersion and invasion.

In addition to the evidence given above, Weaver and Kramer (44) and Aikman (1) report a considerable spreading of *Quercus macrocarpa* in eastern Nebraska since settlement, and Weaver and Kramer point out that the root habits of this species are especially well adapted to development on well drained and aerated soils (*cf.* fig. 23). In contrast to burr oak, *Ulmus americana* seeds widely and grows quickly under favorable conditions and is probably the primary invading forest species in central Iowa at the present time. *Ulmus*, however, will not invade vigorous sod, even that of *Poa pratensis*, and its spread depends upon suppression of sod by *Rhus* or other shrubs, or by erosion, grazing or cultivation (figs. 6, 22). Once established, the elm encourages the spread of other species which may be expected to become dominant on all but flood plain sites.

The prairie soils, both immature and mature, are characterized by a microflora that differs sharply from that of the forest soils. One of the authors has recently discussed certain aspects of this problem (22, 23), and shown that the absence of mycorrhizal fungi may prevent the growth of forest species on prairie soils (fig. 17). White (45) and others have reported similar results. Whatever may be the physiological action of mycorrhizae, the absence of their component fungi would delay forest invasion and render improbable the occasional long jumps that would make rapid invasion possible.

Norman and Moody (26) have shown that the organic matter of forest and prairie soils differs in quality as well as quantity, and that forest organic matter is more active and capable of reducing twice as much hypiodite as that of the prairie. Forest soils students know well the differences between humus types in various forests, and Rayner (29) has suggested that certain types of organic matter decomposition and humus formation may produce substances toxic to trees and to mycorrhizal fungi. Recent work suggests strongly that the roots of conifers are dependent on growth substances secreted by certain fungi or upon certain products resulting from active organic matter decomposition by these fungi. In a continuation of the work of Rayner, Neilson-Jones (25) has obtained evidence that organic compounds toxic to conifers are formed in moorland soils. Conditions are too different to make these results directly applicable to the grasslands discussed here. The authors, however, feel that studies of differences in both the organic matter and microflora of grass and forest soils should be continued. Such studies may help to explain why forest planosols are reforested with relative ease whereas contiguous grassland planosols are invaded slowly, even where the grass is disturbed.

Fire as a Factor Favoring Subclimax Prairie. There can be little doubt that the recent widespread invasion of forest on the prairie, and of other woody plants into areas of grassland in western United States, has been due to changes following settlement. Where the sod has not been broken these disturbances are due mainly to grazing and the use or disuse of fire. The rapid recent spread of tree and woody species on the Edwards plateau in Texas (9) and the invasion of the pinon-juniper and ponderosa pine types into grassland in Arizona (21) are both ascribed to the stoppage of grass fires and to the reduction of grass competition by grazing. In most instances these two factors act together and it is difficult to disentangle the effects of one from the other. We are inclined to believe, however, that the rapid forest advance in western Iowa has been due chiefly to reduction in grass cover by grazing and plowing rather than to prevention of fires. This belief is supported by the surveyors' notes of oak spreading into the prairie in spite of fire, and by the exposed position of younger forests on the Wisconsin drift (fig. 12). Acceleration of invasion cited by Gleason (12) and others as due to fire control could equally well have been effected by intermittent overgrazing.

The role of fire in modifying the forest-prairie boundary prior to settlement is difficult to evaluate. The effects of fires on forests have been more extensively investigated than the effects of fire on grasses. Among those who have written on the prairie-forest relationship the opinion generally prevails that fire has been an important factor retarding forest development. How-

ever, from the literature one can gain evidence for any stand desired (14). The effects of fires would undoubtedly vary with their frequency and severity and would depend upon whether the tree species were of the sprouting or non-sprouting variety and how well insulated the inner bark and cambium were from the short but intense heat of the prairie fires. Transeau (38) expresses the following view: "Fires favor the persistence of prairie species in contrast to tree species. Prairies preceded prairie fires. Whenever one searches the historical literature describing the period of settlement one is impressed by the frequent widespread fires usually ascribed to the Indians. Fire as an ecological factor, seems to boil down to this: that in forest climates it retards development, and may result in scrub, but it does not result in prairie. In a prairie climate it helps to maintain and perhaps rarely enlarges the prairie."

Assuming that fire retards forest invasion, its effect on prehistoric prairie-forest relationships would depend upon frequency and severity. Although no evidence is at hand, it is doubtful whether lightning fires were of any great importance in the prairie peninsula because rain generally accompanies lightning. Thus prairie fires would originate chiefly with the Indians. There is considerable evidence that Indians burned the prairies yearly as a means of hunting the bison, but considering the area of the prairie, and the relatively small numbers of Indians and Indian villages, it does not seem reasonable, if fire were the principal factor, that in this extensive upland prairie with its interlacing wooded streams there should be no more extensive areas of forest invasion. A reasonable conclusion seems to be that fire probably played a local role in retarding forest advance, but that its influence was secondary to other factors and has been over-stressed.

Soil Reaction. On the immature soils of the Wisconsin drift and of the deeper loess deposits the high calcium content of the subsoil tends to retard tree growth. In certain local prairies of the southeastern and southern United States also the percentage of alkaline or saline salts is high. Various authors have suggested that restricted growth on these sites is due to unavailable iron and other minor elements, to insolubility and unavailability of phosphorus, to unfavorable calcium-potassium-sodium balance, or to toxic concentrations of calcium, sodium, potassium, chloride, sulphate and other ions. Most conifers with the exception of *Juniperus* and a few others are seriously affected, especially in the seedling stage, by high concentrations of soluble salts. Among the hardwoods there are more species adapted for growth on alkaline soil (8), but these are usually not adapted to withstand heavy competition in the seedling stage. The problem is further complicated by the effect of organic matter in decreasing injury on alkaline soils and by the fact that many soils derived from limestone, chalk and marl are heavy and possess

poor internal drainage and aeration. The degree of plant injury and soil pH are also sometimes related to and vary with the moisture content of the soil (13).

In pot experiments at Ames *Pinus banksiana* died during the first season on an alkaline Webster surface soil, but grew well on acid prairie soils when inoculated with mycorrhizal fungi. Seedlings of *Quercus borealis* were

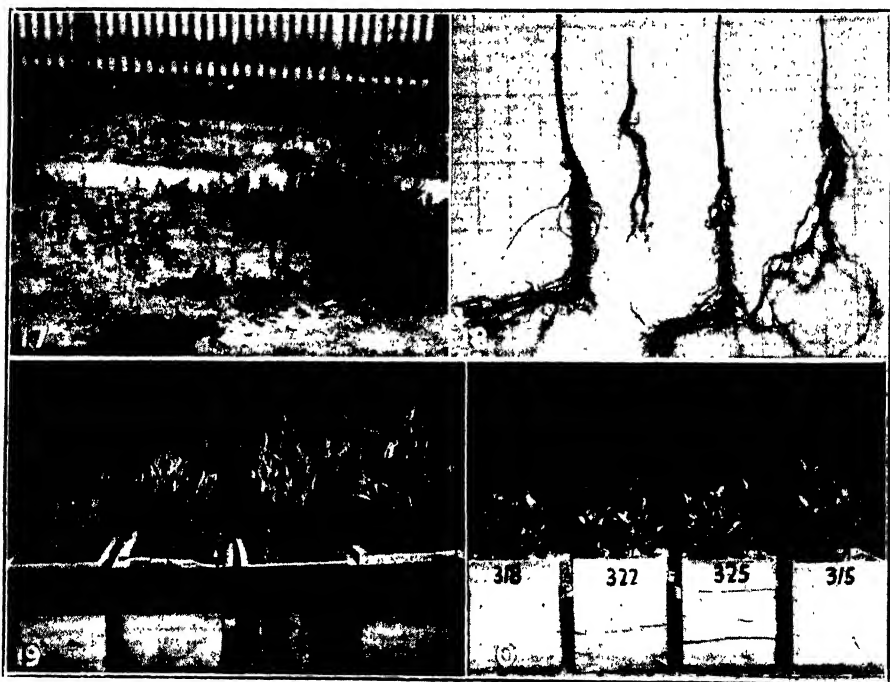


FIG. 17. Seedlings of *Picea Abies* on prairie soil. Dead and dying plants non-mycorrhizal; vigorous plants inoculated with mycorrhizal fungi from mulching material. FIG. 18. Growth of *Quercus borealis* seedlings in prairie and forest, surface and subsoils. Left to right; grown in prairie surface soil (Clarion A); prairie subsoil (alkaline, Clarion C-horizon); forest surface (Lindley A) and forest subsoil (acid Lindley C-horizon). FIG. 19. Response of *Avena sativa* on O'Neill soil to nitrogen fertilization. Left to right: none, 40, 80, and 160 lbs. NH_3 per acre. FIG. 20. Response of seedlings of *Fraxinus lanceolata* to nitrogen fertilization. Soil acid; fertilizers as in figure 19.

chlorotic, stunted, and failed to respond to fertilization on the alkaline C-horizon of a Clarion prairie soil, but were normal in appearance and responded to added fertility on the acid subsoil of Lindley (forest) or the neutral subsoil of Tama (prairie). The root systems of the seedlings on Clarion C were very poor, short and unbranched (fig. 18). Alkalinity is stressed as a factor favoring the black-land prairies of Alabama (24) and the steppes of Hungary (35). Like poor internal drainage and aeration, an

alkaline subsoil is most injurious to the deep rooted species of the forest climax.

Soil Fertility. It is considered typical of xeroseres that the climax formation occupies the most fertile as well as the most mesic sites. In the mature, till soils of the Illinoian and older glaciations the virgin forest climax soils are frequently more fertile than the grassland soils, although their agricultural value may be reduced by their greater slope and tendency to erode. In the immature soils of recent drift or deep loess deposits, however, the grassland soils tend to be markedly better, particularly in nitrogen content.

TABLE 1. *Average total nitrogen content of the surface 2,000,000 pounds of some prairie and forest soils of Iowa.*

Vegetation	Series	Texture	Nitrogen, lbs. per acre
Prairie	Marshall	Silt loam	4,029
		Silt loam	5,600
Prairie	Clarion	Loam	4,368
		Silt loam	4,986
Prairie	Webster	Clay loam	6,762
		Silt loam	8,633
Prairie	Carrington	Loam	3,756
		Silt loam	4,606
Prairie	Clyde	Silt loam	7,157
		Silty clay loam	7,929
Prairie	Grundy	Silt loam	4,253
		Silty clay loam	4,971
Prairie	Knox	Silt loam	2,117
Forest	Clinton	V.f. sandy loam	2,050
		Silt loam	2,506
Forest	Fayette	Silt loam	2,300
Forest	Marion	Silt loam	2,229
Forest	Lindley	V.f. sandy loam	1,733
		Silt loam	2,226
Forest	Ames (Conover)	Silt loam	2,150

Nitrogen analyses of important prairie and forest soils of Iowa by Walker and Brown (42) are given in table 1, and show an average nitrogen content for the prairie soils that is two or more times that of the forest soils. Note particularly the Ames soil, developed from the same parent material as the Clarion, or the Marion from the same material as the Grundy but containing in each instance about half as much nitrogen. Note also that the Knox silt loam, one of the types being invaded in western Iowa, shows a nitrogen content comparable to that of the forest soils. The high nitrogen content of the grassland soils is assumed to have accumulated under grassland cover and to be associated with the more stable organic matter forms of the prairie soils.

Nitrogen is recognized as a major fertility factor for grass development; in contrast, experiments by one of the authors have shown that tree seedlings did not respond to added nitrogen on several Iowa soils when the initial nitrogen content of the soil was more than about 2,000 pounds an acre in the surface 2,000,000 pounds of soil. The responses of two tree species to nitrogen fertilization on an O'Neill soil containing 1,900 pounds of nitrogen are compared in table 2 and in figures 19 and 20 with the responses of *Avena sativa*, used to represent a quick-growing grass. While the growth of *Avena* was increased 700 per cent on this rather infertile soil, the growth of *Fraxinus lanceolata* was unaffected and the response of *Quercus borealis* was of doubtful statistical significance.

Cowles (6) has suggested that prairie tends to change the soil in a direction which favors grass at the expense of forest. For the fertile, immature

TABLE 2. *Relative responses of a cereal grass and of two tree species to nitrogen fertilization of an O'Neill soil.*

	Dry weights of seedlings as a percentage of the check		
	<i>Avena</i>	<i>Quercus</i>	<i>Fraxinus</i>
None	100	100	100
40 # NH ₃ per acre	467	119	101
80 # NH ₃ per acre	801	115	95
160 # NH ₃ per acre	820	130

prairie soils of Iowa and northern Illinois we advance the thesis that high nitrogen levels, built up in these soils during prehistoric, grassland climate cycles, are under present conditions an important factor favoring prairie species in their resistance to forest invasion. The high nitrogen content of these soils increases the density of the grass cover and results in such rapid resodding of disturbed areas that there is little opportunity for forest seedlings to become established. The dense growth and fibrous root systems of the grasses quickly remove surface moisture below the wilting point during even short dry periods. In addition they may reduce the level of available phosphorus (22) and/or other elements (45) to levels critical for tree seedling growth, and raise the carbon-dioxide content of the soil (16) to a point injurious to tree roots.

Erosion has long been recognized as having a favorable effect on forest invasion; an effect which is usually assigned to better drainage and to protection in the gullies and rough lands from the drying effects of wind. Under our theory the removal of the grass cover, and the removal of the high-nitrogen A-horizon which favors its return, become major parts of the effect of erosion. Even when the nitrogen content of eroded areas is reduced below the optimum for trees, the reduction or elimination of grass competi-

tion makes such spots available for invasion (fig. 22). The movement of invading forests along steep-banked prairie streams has probably depended as much upon this effect of erosion (figs. 11, 12, 21) as upon any single factor.

Soil Aeration. Subelimax prairie is found typically on flat alluvial or till plains, and many authors have called attention to the poor surface and internal drainage of the soils formed on these sites. Englemann (7), for example, has stressed drainage as the cause of subelimax prairie. His discussion of the prairies of Jackson and Perry counties in southern Illinois is



FIG. 21. Forest distribution along the Des Moines River, Boone County, Iowa. The Ames soil in the foreground has been cleared of forest, as have the pastures above the farther bluffs. Present woodlands are on the steeper Lindley soil. Trees on the Wisconsin till plain of the background are farmplot plantings.

noteworthy for careful observations in a district where prairie has apparently persisted for many thousands of years in a distinctly forest climate, and for its early date (1863) which enabled the writer to consult original settlers and to observe relatively undisturbed plant communities. He reports that prairie was restricted to the undissected till plains, and that these were being invaded from the rolling lands along the streams, with invasion of the narrower strips of prairie being complete. The timber on these flat lands, however, was a poorly developed growth of *Quercus stellata*, *Q. marilandica*, and *Q. palustris*, the first two considered indicative of dry and the last of

wet lands. Englemann attributed the persistence of the prairie to poor surface and internal drainage, and reported that the "post oak flats" alternated between standing water in early summer and severe drought in late summer, so that only the more resistant trees were able to exist on these former prairies. In the soils maps of Jackson county (27) the mature prairie soil on Illinoian till, thinly covered with Peorian loess, is classed as Cisne. Where the till plain has been invaded by oak-hickory timber it is mapped as Wynoose. Timber on rolling land along the streams developed the Bluford soils, and grass the Hoyleton series. Englemann reports that the Hoyleton soils, which he called "barrens," had been invaded by oak in 1860, at a rate which seemed to class their grassland cover as a disclimax maintained by fire. The level Cisne soils, however, have probably resisted forest invasion throughout most of the 150,000 or 200,000 years since the retreat of the Illinoian glacier. The force of this resistance can be judged by the fact that the bands of Wynoose soils bordering the prairie are rarely more than one-half mile wide, indicating an average invasion rate of about one foot per century.

While the Cisne and Wynoose soils are developed over level, Illinoian till, they are actually formed from a sheet of Peorian loess 3-4 feet thick (34). Ten miles south of the Jackson county prairies and post-oak flats, this same loess on unglaciated hills was covered with a luxuriant forest of *Quercus alba*, *Nyssa sylvatica*, *Liriodendron tulipifera*, and associated species, with *Acer saccharum*, *Fagus grandifolia*, and *Magnolia acuminata* prominent in protected sites. Transeau (37) classes *Liriodendron tulipifera* as a critical species of the eastern hardwood climax forest, yet one of the writers recalls a specimen of this tree growing on an exposed ridge of Ava loess at the south boundary of Jackson county that was 6 feet d.b.h., 90 feet to the first limb and more than 120 feet high. With climate and parent soil material identical, only topography and its effects remain to explain the sharp break between the prairies and scrub oak of the till plains and the adjoining original forest cover represented by this specimen.

Partly because of the methods of their deposition, and partly because of the type of weathering which occurs in them and the absence of erosion, flat lands tend to be fine-textured and to develop at maturity into planosols with a heavy, impervious B-horizon. If the climate is such that grass is the initial vegetation of these plains, or if the forest is destroyed during dry cycles, invasion by forest becomes difficult. In the absence of stream dissection and enough sheet erosion to carry away the clay particles formed by weathering, the difficulties of invasion increase sharply with time as the clay materials are leached downward to form a shallower and more impervious B-horizon. Prairies on flat lands thus tend to perpetuate themselves by forming planosols as well as by direct competition.

The importance of topography in soil formation is illustrated in the forest profiles formed on the loess soils of southeastern Iowa. On flat uplands, Marion soils are formed and the forest is composed of *Quercus stellata*, *Q. marilandica*, *Q. bicolor*, and *Q. imbricaria*. With slopes up to 5 per cent Weller soils are formed with a covering of *Quercus alba* and *Carya ovata*. On steeper slopes the Clinton soils support the last two plus *Quercus borealis* and *Tilia americana* as dominant species. All of these soils have developed from the same parent loess, but the level Marion has a planosol profile and a distinctly inferior forest cover which has a record of very slow invasion into the almost equally impervious prairie soils of the Edina and Putnam series. Where slope changes are abrupt the changes in vegetation are equally abrupt and the species of the more rolling lands may disappear within 50 feet.

The relationships of southern Illinois and southeastern Iowa are general, not only throughout the prairie peninsula, but for the subclimax and border line grasslands of the world. In Hungary (35), Australia (28) and Africa (11) as well as Alabama (24) and Arkansas (41), prairies on the more mature soils have been driven back to flat areas of impervious silts and clays. The prairies of Arkansas and of Louisiana for example are found on flat, heavy, Port Hudson terrace soils (fig. 25). These terraces were formed from glacial clays deposited in middle pleistocene times (40), and are therefore comparable in topography, texture, and age to the prairies of the older till plains.

Although trees of various species will grow under moisture conditions ranging from permanent swamp to semi-desert, the root systems of trees seem to be generally inefficient in both soil-contact area (fig. 18) and level of physiological activity. It seems probable, therefore, that it is not poor drainage alone, or even alternating wetness and dryness, which limits forest growth on these prairie soils, but rather the unfavorable oxidation-reduction relationships of fine-textured, wet soils. Thus we find the well aerated Knox and Monona soils of western Iowa invaded much more rapidly than the impervious Cisne of southern Illinois; in central Iowa the deep, frequently rather sandy soils of the Clarion series on Wisconsin till have been invaded more rapidly than the impervious Putnam soils formed on the older Peorian loess over Kansan till in southern Iowa, and throughout the prairie-forest borderline small differences in elevation, drainage, and aeration markedly affect forest invasion (figs. 24, 25).

Patton (28) stresses soil texture and topography as major factors in the distribution of grasslands and forest in Victoria. Forest is reported on the coarser-textured soils, even when rainfall conditions are unfavorable, while subclimax prairie persists on impervious plains. Stoeckeler and Bates (36) ascribe the beneficial effects of sandy soils in the shelterbelt region to their

greater free moisture content. Turner (39) stresses soil aeration as an important factor affecting growth rates of trees. Under critical conditions poor growth means poor survival, and we feel that poor soil aeration, due to poor surface drainage and particularly to impervious, clayey soils, is the most important single factor restricting the spread of forests and favoring the persistence of subclimax prairie throughout the world.

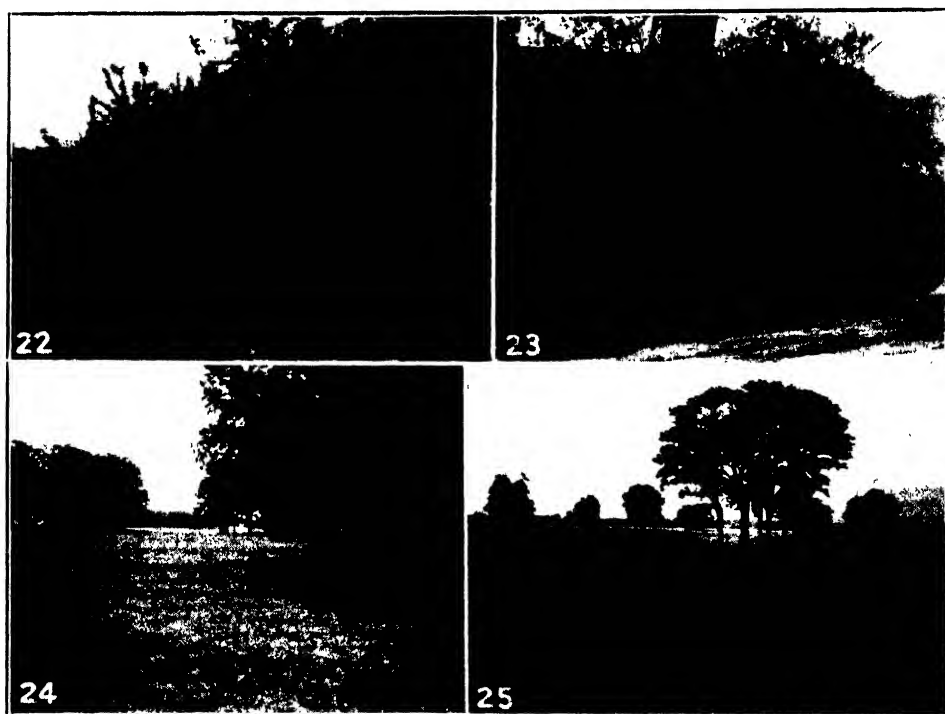


FIG. 22. Pure stand of *Ulmus americana* on subsoil exposed in road cut; west exposure; no evidence of seepage. Jasper County, Iowa. FIG. 23. Exposed roots of *Quercus macrocarpa* in western Iowa. Medium-sized roots were abundant at the 9-foot level. FIG. 24. Oak-hickory forest on swells of the more porous Clarion soils with swales of compact Webster originally in low prairie. Boone County, Iowa. FIG. 25. Trees on hummocks; Port Hudson Terrace prairies of southeast Arkansas.

The effects of soil aeration on forest-prairie competition cannot be explained until we know more about the physiology of roots and particularly of tree roots. A space factor is undoubtedly concerned, with the heavier growth of the forest requiring a deep root system for an adequate water supply during periods of stress. It seems probable, however, that questions of fine root growth and level of physiological activity are involved; that tree roots are relatively inefficient and, in some of the more xeric species at least, susceptible to the effects of oxygen deficiencies (15) or carbon dioxide

accumulations (18). If it should develop that the roots of the more xeric hardwood forest trees are particularly susceptible to carbon dioxide accumulation, the data of Howard (16) would gain added significance to the problem of invasion of the prairie. He found soils under grass containing up to five times as much carbon dioxide as his cultivated control soils. Such an accumulation in soils of compact structure and slow rates of gas exchange might be the determining factor in the survival of tree seedlings in sod.

DISCUSSION

Pollen analyses from all parts of the prairie peninsula are in agreement in showing a very general spread of northern coniferous forests throughout the region during each of the glacial periods. In Iowa pollen analyses (20) and buried soil profiles (33) show that the interglacial periods have been dominated by grass rather than by deciduous forest, indicating that the soils and/or climate of the state have not been generally favorable for invasion by southern forest species during pleistocene times.

Picea forests were present in Iowa following the late Wisconsin glaciation and may have been general. Unfortunately for our studies, most peat deposits are surrounded by moraines or other formations relatively favorable to forest. *Picea* will grow, however, in flat, wet soils, and pending analyses of peat from the open till plains the authors are inclined toward the assumption that these also were at least partially covered with coniferous forests. Such an assumption must account for the absence of any residue of a forest profile in the prairie soils. The prairie fauna, from earthworms to badgers, is so predominantly burrowing, however, as to seem able to rework shallow profiles in the period available.

With rising temperatures the spruce forests should have been replaced by oak-pine or oak. Instead *Pinus* pollen never exceeded five per cent at this stage in Lane's Hancock County bog (19), and *Quercus* pollen was exceeded by grass and weed pollens indicative of a savanna rather than a closed forest. It seems highly probable that the till plain went directly to prairie during this time, as it apparently had during earlier interglacial periods. The high initial lime content of the till plain, and its flat topography without protected or disturbed areas for ready invasion, as well as its poor soil aeration, would have favored grass rather than oak during this increasingly xeric period.

In the 8th and 7th feet of Lane's bog, graminaceous pollen increased from 23 to 60 per cent and *Quercus* dropped from 20 to 4 per cent. Such a change clearly indicates a severe dry period. It is noteworthy that *Quercus* pollen averaged 4 per cent from the 7th foot of this bog to the top, suggesting that pollen was coming from the groves still present in the lee of Twin Lakes one to two miles north and west of the bog. Many data indicate that this dry

cycle was general; its probable date, 5000 to 8000 years ago. During this dry period grass undoubtedly became established on much former forest or savanna occurring on morainal hills and eroded slopes. The Hoyleton soils of southern Illinois and the morainal hills of northern Illinois may well have been deforested at this time, and the forests driven back behind the streams, lakes, and other fire-breaks, or to protected areas, that are mentioned above as showing in the distribution of mature forest soils but not always in the more recently established, original forest cover.

Although pollen analyses indicate a more mesic period between about 4000 and 1600 years ago, soils data from central Iowa indicate that the climate was in the main that of a grassland climax with only limited forest invasion during the period. A generally warm-dry climate during the Middle Ages is reasonably well documented by tree rings, historical records, Nile valley floods, remains of the Greenland settlements, etc. (4). The end of this dry cycle at about 1100 A.D. probably marked the beginning of the current forest climax climate for Iowa and the western base of the prairie peninsula.

During the last 700 or 800 years forests had covered townships in north-eastern Iowa, advanced one to four miles from the main streams of central Iowa, and advanced as scattered trees and clumps in western Iowa at the time of settlement of the state. The disturbances of settlement, mainly, we feel, periodic over-grazing of prairies and pastures, have resulted in spectacular forest advances in western Iowa during the last 50 years. The early advances were as rapid as could have been expected against the competition of established and vigorous prairie sod, but they were limited to deep, well aerated soils. Swales of poorly aerated Webster soils were by-passed in central Iowa (fig. 24), and invasion of mature or nearly mature planosols in southern Iowa and Illinois was negligible. Afforestation, including recent invasion, in western Iowa has followed a belt not far behind the Missouri river bluffs which perhaps represents a gradation of the loess (34) into particles neither too coarse and therefore dry, nor too fine and poorly aerated.

The remainder of the prairie peninsula remains, as it probably has during most interglacial time since the Aftonian, a subclimax or edaphic climax maintained primarily by its flat topography and its impervious, poorly drained and poorly aerated soils. If the present climate lasts for the necessary millions of years until the till plains are dissected and their heavy surface and subsurface soils eroded away, we may expect the disappearance of the prairie peninsula.

SUMMARY

Undisturbed Iowa forests survived the recent drought years without injury, and forest is spreading and maintaining itself throughout the state

under present climatic conditions. Oak-hickory forest is therefore considered to be climax, from a line somewhere near the Missouri and Little Sioux rivers eastward. In western Iowa, where the climate approaches that of a prairie climax, soil factors become increasingly important, and forest potentialities are limited to the coarser-textured, better aerated soils. Forest in this area requires no protection, however, from the full force of sun and wind under present climatic conditions, and is currently invading both disturbed and undisturbed areas.

General and local evidence from glacial varves, tree rings, pollen analyses, soils distribution, and other sources indicates that the climate of Iowa during late-glacial and post-glacial times has changed from boreal through oak-hickory forest climate to grassland climate, and that the current forest climate has probably existed for only 700 to 800 years. For perhaps 5000 years preceding this recent shift the climate of Iowa was predominately that of a grassland climax, with the forest driven back to areas of deeper soils sheltered from fires and prevailing winds.

The prevalence of prairie in Iowa and Illinois is not, however, due to this recent xerothermic period, but dates probably to the soils disturbances initiated by the first or Nebraskan glaciation. The prairie peninsula is considered to be a subclimax associes maintained by the soils and topography of the glacial till plains. On the unleached soils formed from deep sheets of Peorian loess and Wisconsin till, the high lime content of the soils and past xerothermic periods have favored prairie grasses and legumes which have in time built up a high nitrogen and organic content in these soils. This content now stimulates the growth of grasses at the expense of invading tree seedlings. On the leached but undissected till plains of the Kansan and Illinoian glaciations, planosols of poor surface and internal drainage and aeration have been developed which are distinctly unfavorable for trees, particularly under border-line climatic stresses. Planosol prairies are invaded very slowly and only by the more xeric forest species, even with a distinctly forest climate, and their transformation to oak-hickory climax will probably require extensive erosion to establish drainage and permit development of new and less mature soil profiles. These prairies may therefore be considered to be a semi-permanent, edaphic, but not climatic, climax.

The invasion of forest along streams, which has been cited as evidence of a forest postclimax dependent upon protection, is considered to be related in the older soils to increased drainage and soil aeration, and in the less mature to the removal of the high-nitrogen surface soils which are relatively much more favorable for the growth of grass than of the slow-growing and vulnerable tree seedlings.

The relationships shown for Iowa are present throughout North America and in Europe, Africa and Australia. In local areas prairies are maintained

by sandy or gravelly soils too dry to support forest. The vast bulk of the peninsula and of other subclimax prairie, however, is found on silty or clayey plains of glacial, alluvial, or other origin. Poor soil aeration caused by fine-textured soil and poor drainage is probably the most important factor in the persistence of these subclimax prairies.

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MORPHOLOGICAL OBSERVATIONS ON THE TOMATO PLANT¹

F. W. WENT

Even though a number of papers have been published on the abnormal morphology and teratology of the tomato plant (Caldwell 1930, Dana 1939, Masters 1869, Penzig 1894, Rischkov 1938, Schlösser 1936, Worsdell 1915) there are surprisingly few in view of the importance of the tomato as a major crop plant on the one hand and its uncommon variability in a morphological sense on the other hand. During the last four years about two thousand full grown tomato plants and 40,000 seedlings were observed in the greenhouses of the California Institute of Technology, grown in part under well controlled conditions, and in the following article morphological observations on these plants will be described. Some of these observations were systematically carried out on all plants, but those on the rarer teratological cases were entirely incidental.

Most observations were made on "San Jose Canner" tomatoes, *Lycopersicon esculentum*, but additional work on "Marglobe" and other varieties has shown that many of the described phenomena are not restricted to one variety only. The tomato seeds were sown in flats in washed sand, 100 per flat, and were watered with nutrient solution after germination. The almost complete absence of any segregation of such characters as dwarf, potato-leaf, yellow leaf, and the great uniformity of growth-rate and response to external factors (Went 1943) all point towards the essential homozygosity of the seed. The abnormalities were found in ever changing proportions, indicating that they were modifications and not genetically determined. Moreover, most of these abnormalities occurred only in one stage of development, and before and afterwards the plants were perfectly normal.

Seedlings. During germination the two cotyledons unfold and enlarge. Syncotyly is very rare (less than 1 in 1000) and tricotyly is rarer than in most plants (8 in 3300). About one week after germination the first two foliage leaves, which were already initiated in the embryo, grow out. Occasionally (less than 1 in 2000 plants) these two first leaves have merged into a beaker-like structure or even into one peltate terminal leaf, without trace of a terminal bud between them. A cotyledonary bud develops in such plants and takes over the main stem function. In such cases the two leaf primordia

¹ The author is indebted to Mrs. M. O. Carter for the preparation of the drawings in this paper.

must have merged and overgrown the terminal meristem. This was never observed in any other stage of development of tomato plants.

The following most remarkable abnormality was observed three times: After normal germination the first two foliage leaves developed. No terminal nor axillary buds were present; even under the microscope no trace of them was visible. Therefore these seedlings did not develop beyond the two-leaf stage. But both cotyledons and leaves continued to grow in surface and thickness. Instead of falling off after a month the cotyledons remained alive and attached to the plant throughout its life span, which was 3-6 months. The root system seemed perfectly healthy and normal, and well developed. Similar cases were described by de Vries (1903, p. 322) for *Helianthus*, *Pentstemon*, and *Cannabis*. Apparently these seedlings had completely lost the ability to form buds anywhere. In normal plants decapitation and debudding lead to the formation of numerous adventitious buds on the callus overgrowing the wounds and on the upper surface of the leaf rachis. But these budless seedlings showed no trace of such regeneration. Nor did they regenerate anything but a slight callus on wounds produced on leaves or stems, even after treatment with auxin paste.

Two seedlings were observed which were completely budless, like the ones just described, but lacking even the two primary leaves. They consisted only of roots, a hypocotyl, and two cotyledons.

Phyllotaxis. The leaves of the tomato are inserted on the stems with a typical $2/5$ divergence (Hayward 1938; sometimes referred to as $3/5$: Caldwell 1930, Schlösser 1936). There is no favored direction of the foliar spiral: out of a group of 50 plants 25 had a left- and 25 a right-hand spiral. It seems to be entirely left to chance where the larger gap between the first four leaf primordia appears. As mentioned before, the first two foliage leaves are practically opposite and develop simultaneously; the next two leaves are sometimes almost opposite, but more often they are inserted at different levels and have a divergence of less than 180° . Beyond that a normal $2/5$ spiral appears.

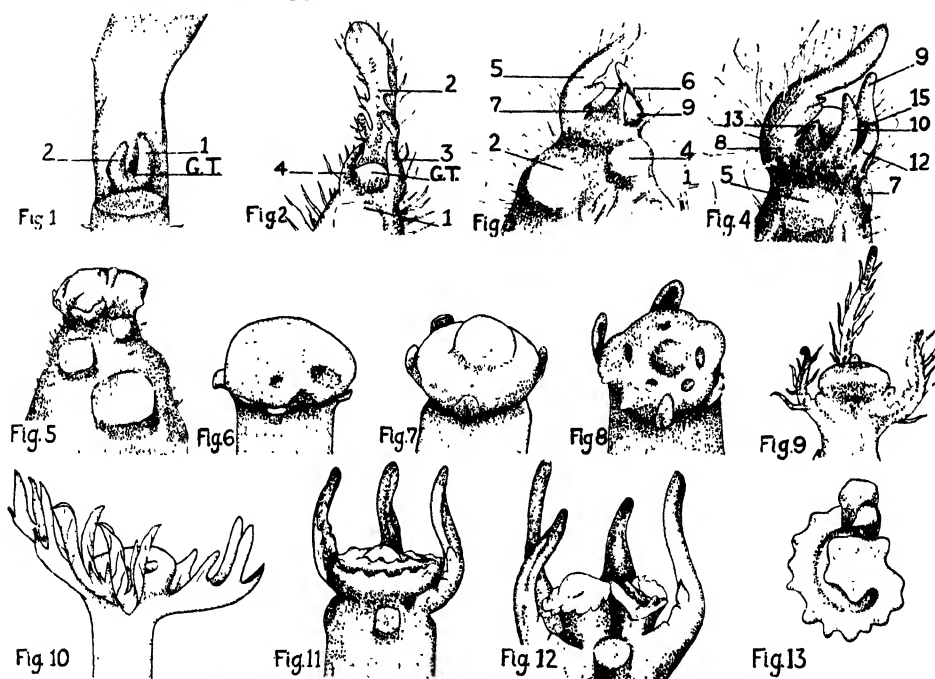
In 17 of 2200 seedlings the first two leaves were not opposite, and a regular $2/5$ phyllotaxis started actually with the first leaf. Almost all these 17 plants were taller than those with opposite primary leaves.

In tricotyly the first three leaves develop simultaneously and are of the same size and are practically whorled, alternating with the three cotyledons. In one plant three whorls of three leaves each developed after the three cotyledons. Immediately above the third foliar whorl the stem was bifurcate, the two branches having normal foliar spirals in opposite directions.

In more than 90 per cent of all plants the direction of the foliar spiral does not change up to the first flower, so that the direction once established

in the seedling persists. But in less than 10 per cent a reversal of the foliar spiral occurs between the fifth and fifteenth leaf. Lateral shoots from the main stem have an equal chance to follow a left- or a right-hand spiral, irrespective of the direction of the foliar spiral in the main shoot, and no pattern in their appearance was found. This also attests that the left- or right-hand character of the foliar spiral is fortuitous, and is not an inherent or inherited characteristic of each individual.

When the seedling shoot emerges from the soil, microscopical examination shows only two opposite leaf primordia enclosing a flat and very small

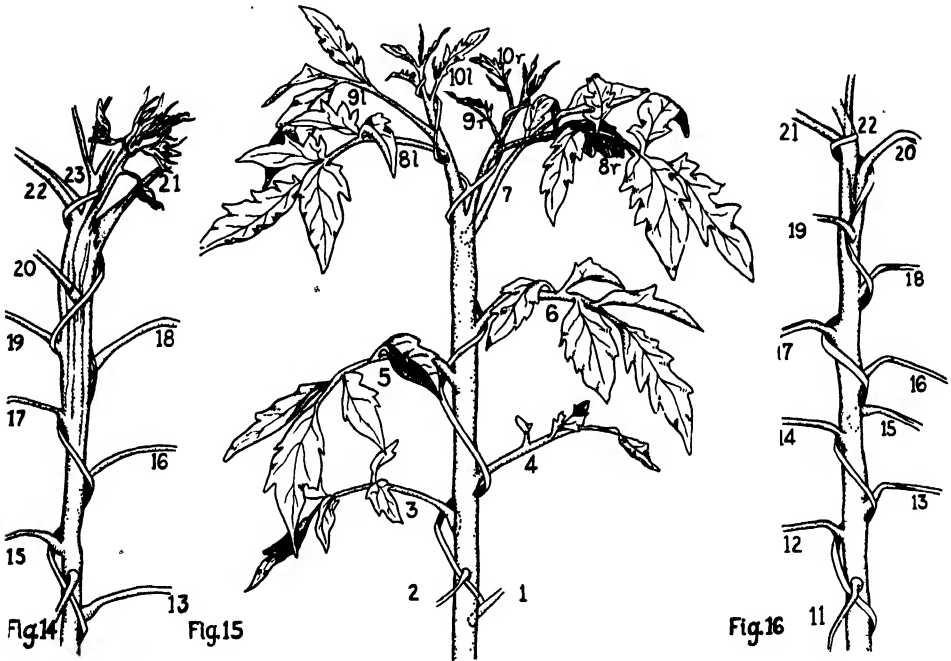


FIGS. 1-4. Vegetative growing points (G.T.) in young tomato plants. Numbers refer to order number of leaf primordia. The larger leaves have been removed and their scars are numbered. FIG. 5. Normal flower primordium (fasciated) formed after 16th leaf primordium. Lateral flower primordium without subtending bract just below terminal flower. FIG. 6. Flower primordium, arrested in further development, formed after 4th leaf. FIGS. 7 and 8. Flower primordia laid down after 7th and 8th leaf. FIGS. 9-13. Flower primordia formed after 10th-13th leaf.

growing point (G.T. in figure 1). From the next stage on, when the first leaves are just starting to expand and are only a few millimeters long, the growing point is dome-shaped, and the leaf primordia appear in spiral order some distance below the dome. Figures 2, 3, and 4 show the growing point in different stages of vegetative development of the plant. The leaves are numbered in the order in which they appeared on the growing point. These figures show that the primordia are never in contact with each other, and

throughout their development remain separate. After 14–20 leaves have been initiated, the growing point broadens and is transformed into a terminal flower primordium (fig. 5). Occasionally, as seen in this figure, a small number (1–3) of lateral flowers are initiated as axillaries of bracts and thus continue the foliar spiral. The subtending bracts of these lateral flowers may or may not be apparent, and under the proper conditions (high night temperatures) these bracts can develop into normal leaves (cf. Went 1943).

In some plants the direction of the foliar spiral reverses without any apparent reason. One such case is shown in figure 15, in which the spiral was



FIGS. 14 and 16. Exceptional foliar insertion on young tomato plants below their first inflorescence. Whereas up to the 18th or 19th leaf a normal right-hand $\frac{2}{5}$ spiral exists, indicated by the ribbon following the insertion, (leaf 18 just above leaf 13), this spiral reverses for the next 5–3 whorled leaves. Stem becomes much creased above 18th leaf. Axillary shoots from the highest leaves not drawn. FIG. 15. Dichotomy of tomato stem. Right hand foliar spiral up to fifth leaf, beyond that left hand spiral which continues in both shoots.

right-hand up to the fifth leaf, but beyond that changed to left-hand. In other cases, like in figures 14 and 16, the spiral reverses in connection with the formation of the first flower, which will be discussed later.

Figure 15 also shows another abnormality, namely, true dichotomy of the stem. Caldwell (1930) also described dichotomy in tomatoes. Although many authors (e.g., Velenovsky 1905) reject the existence of true dichotomy in angiosperms, the case of figure 15 seems well-founded. After the seventh leaf

the stem branches into two almost equal forks, each with a normal phyllotaxis. In both the same left-hand spiral of the 5th–7th leaf is continued. All leaves, including numbers 5, 6, 7, 8r, 8l, 9r, and 9l have normal axillary buds, so that neither of the shoots can be considered an axillary shoot. Besides, no trace of a flower primordium or aborted leaf is visible. This is important, since in the tomato most cases of apparent di- or trichotomy arise in connection with flowers, and are axillary buds from opposite or whorled leaves just below the flowers, while the main axis is terminated by the flower.

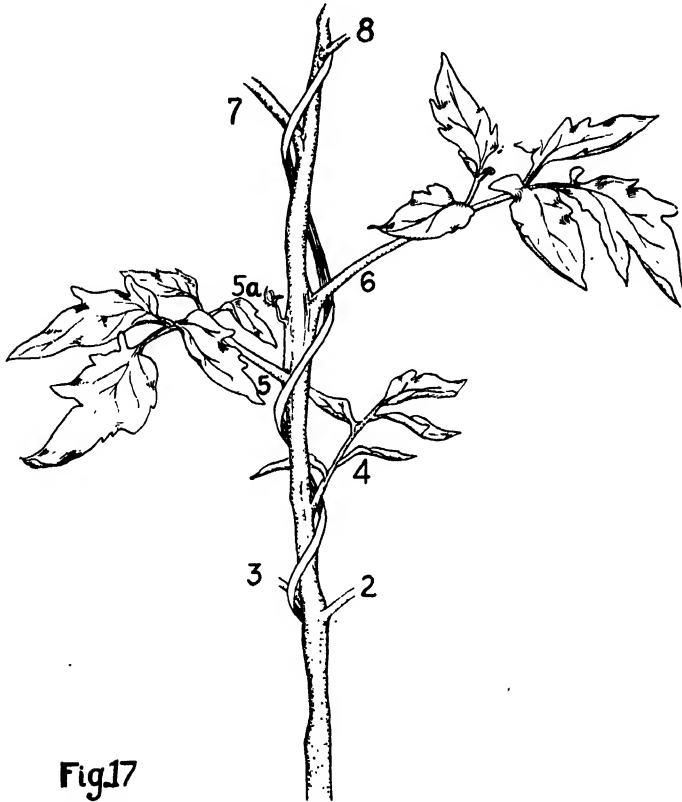


Fig. 17

FIG. 17. Adventitious leaf (5a) not interrupting foliar spiral.

In not more than 10 per cent of the plants which develop dichotomy, an apparent duplication of the leaf immediately below the bisection was visible. In such cases the petiole was inserted with a wide base, and two axillary buds were visible. The end leaflet of this leaf was bifurcate. Here a true connation of two leaves existed. A similar case has been observed in a seedling with the two first foliage leaves grown together along the petiole, and having a forked end leaflet. In one case connation of two opposite leaflets was found. They emerged as one leaflet on the adaxial side of the leaf rachis,

but were still clearly recognizable as two since farther up the leaflet was forked.

Once a true adventitious leaf was observed on a tomato stem (fig. 17). It was very small, consisting of only three minute lobes on a thin petiole, and it did not interrupt the foliar spiral. There was a normal 144° divergence between the leaves immediately below and above the adventitious leaf. An explanation of this case seems simple on the basis of a vertical duplication of a leaf primordium, since the adventitious leaf was inserted almost exactly above the lower leaf.

Another interesting phenomenon observed in tomato plants whenever growing conditions are very favorable, and when both day and night temperatures are fairly high, is the disappearance of apical dominance. As soon as the tomatoes have reached a height of 30–40 cm. all lateral buds start to grow out, and continue to grow. A number of them may reach almost the same growth rate as the main stem, which is not markedly inhibited in its growth as long as there are not too many laterals competing with it. This phenomenon occurs only when aeration of the roots is optimal, as in gravel or coarse sand, or when enough roots have developed above the nutrient solution on plants grown in water culture.

Under the same conditions as are necessary for the abolition of apical dominance, another phenomenon can be observed. This is the formation of from few to many adventitious buds on the rachises of the leaves. This bud formation becomes pronounced only when the growth of lateral shoots is prevented, and it starts on older leaves. These adventitious buds can grow out into normal leafy shoots, but when too many develop per leaf they remain smaller. The same phenomenon has been described for tomatoes by Penzig (1894) and Gustafson (1937).

Flower Initiation. The various stages of the tomato flower primordium are described by Hayward (1938). In older plants flowers may be observed in almost any stage of development, but young plants do not form flower primordia unless at least 13 leaves have been initiated. In exceptional cases (1–5 per cent of all plants) tomatoes will produce a terminal flower primordium in an earlier stage of development. These primordia, however, never develop into normal flowers but remain arrested in their growth at some early stage of differentiation, although the rest of the plant continues to grow. The meristematic cells of such a flower primordium remain isodiametric but enlarge to some extent, so that a stationary and magnified model of a young flower is produced, which abruptly terminates the stem. The internode between primordium and highest leaf may be as long as or longer than the preceding one, so that when the flower development has not progressed so far that the sepals are growing out, it appears as though the main

stem of such a plant had been cut off with a sharp knife. Such abnormal plants are easily recognized in somewhat later stages when the axillary buds of the upper leaves start to grow out. Sometimes some or all of these terminate in the same way. But the stem developing from the highest normal bud will be entirely normal, proving that the abnormality is a modification, and not genetically determined.

In the most extreme cases, observed only a few times, the flower primordium was produced after the second to fourth leaf. One such case is shown in figure 6. The calyx primordia are barely indicated. The meristem has remained indefinitely in the semimature condition, but is clearly different from the rest of the stem tissue in that no hairs or glands have developed on it. The primordia shown in figures 7 and 8 terminated the main stem after about 7 leaves had been formed. The sepals are further developed, and indications of petal primordia are present. When the plants were slightly older before the flowers were formed, almost invariably the sepals started to differentiate as foliage leaves, as indicated by the lateral lobes at their base, which are always absent in sepals. Figures 9, 10, 11, and 12 show such sepals. The transformation to leaves has not been complete since they have not grown out further. In such primordia the place where the carpels should develop is mostly occupied by an undifferentiated meristem, sometimes superficially pitted, the number of pits corresponding with the number of sepal primordia. This phyllody of the calyx can also be observed in lesser degree in normal flowers, especially of plants grown in low night temperatures. Schlösser (1936) has investigated a genetically determined case of phyllody, and Dana (1939) stressed the correlation between virus attack and phyllody of calyx.

In primordia formed from the ninth leaf on, the meristem from which the flower differentiates enlarges to such extent that fasciated flowers or primordia result. Usually the number of sepals is still five, but all other flower parts have considerably increased in number. All different stages have been encountered, from a simple ribbon-like widening (fig. 12) to spirals (fig. 13) and complete ring structures (figs. 10, 11). In the latter petal and stamen primordia are formed both along the outside and inside of the ring-like meristem. In a few primordia (figs. 7, 11) the center of the meristem protrudes in a manner suggestive of continuation of the stem meristem, but not a single instance has been observed in which a recognizable stem was formed in the center of a flower. For this reason it is doubtful whether this central protrusion, which never shows further differentiation, has any morphological significance.

The later the first flower primordium is laid down in the development of the plant, the stronger is the fasciation. Therefore the first flower which fully develops is invariably strongly fasciated. Anywhere from 15 to 50

carpels may develop. Masters (1869) mentions syncarpy. Masters and Penzig consider many of those fasciated flowers as synanthia, but others are due to the natural variability in number of flower parts in the tomato. These supernumerary carpels are arranged, as would be expected from the primordia just described, either in single or branched ribbons, or in rings. In the latter case the center of the flower is occupied by a whorl of sepals, followed centrifugally by whorls of petals, stamens, carpels, stamens, petals, and sepals. Such a case was also described by Rischkov (1938).

Fruits from fasciated flowers are invariably larger and heavier than ordinary fruits which weigh 100–200 g. The heaviest fasciated fruit which developed weighed 675 g. Its shape was comparable to that of a brain, since the ribbon of carpels was folded and branched like the convolutions of this organ. When lateral flowers and fruits are present in the first flower cluster, the fasciation of the end flower is never so extreme as when the latter is solitary. The lateral flowers are mostly normal 6-merous.

It seems that differentiation of carpels is only possible when at least 12 foliage leaves have been formed since germination. With the presence of carpels the full development of sepals, petals, and stamens is correlated. As an exception to the latter rule the first sepals may change over, after their initiation, to foliage leaves. The greater the number of foliage leaves already present on the seedling, the larger these transformed sepals grow before their development is stopped. Examples are seen in figures 10, 11, and 12. In the more advanced stages even an axillary bud is present above each sepal (fig. 9) and the stem axis between the sepals and the primordium starts to elongate. This was also observed by Masters (1869, "apostasis"). Frequently, after the initiation of this whorl of 3–5 calyx lobes transforming into leaves, the growing point forms a new complete and strongly fasciated flower, which usually does not carry lateral flowers. Therefore in a varying percentage of plants, and most frequently in plants growing in high night temperatures, the first flower is surrounded by 3–5 more or less whorled leaves. Such cases are shown in figures 14 and 16. The insertion of these upper leaves at approximately the same height indicates that they do not belong to the ordinary foliar spiral. The following other arguments in favor of their initiation as sepals can be adduced:

- 1) The stem below these whorled leaves is not round, but strongly creased and lobed on cross-section (fig. 14).

- 2) In one group of 40 plants 34 had 16–20 leaves in a normal foliar spiral below the first flower. Six plants had an irregular more or less whorled leaf arrangement below the first flower. All of these had 22–26 leaves, of which 17–19 were placed in a normal foliar spiral, and the upper 3–7 were whorled. Figure 18 shows the distribution curve of the number of leaves below the first flower, and gives clear evidence that the whorled leaves are "extras."

3) Still clearer proof of the different nature of the 3-7 whorled leaves in the six exceptional plants is found in their arrangement. They are not placed in a perfect whorl, but some are inserted higher than the others. In this way a spiral may still be traced through them. In only two of six cases the spiral through these extra leaves was continuous with the foliar spiral in the lower part of the stem, but in the other four cases the spiral changed from left to right or the reverse after the 18th or 19th leaf. Such a reversal in spiral between foliage leaves and sepals is not uncommon and it proves that these upper 3-7 leaves are not started as leaves in the ordinary cycle of leaf initiation in the growing point but belong to a different morphological series.

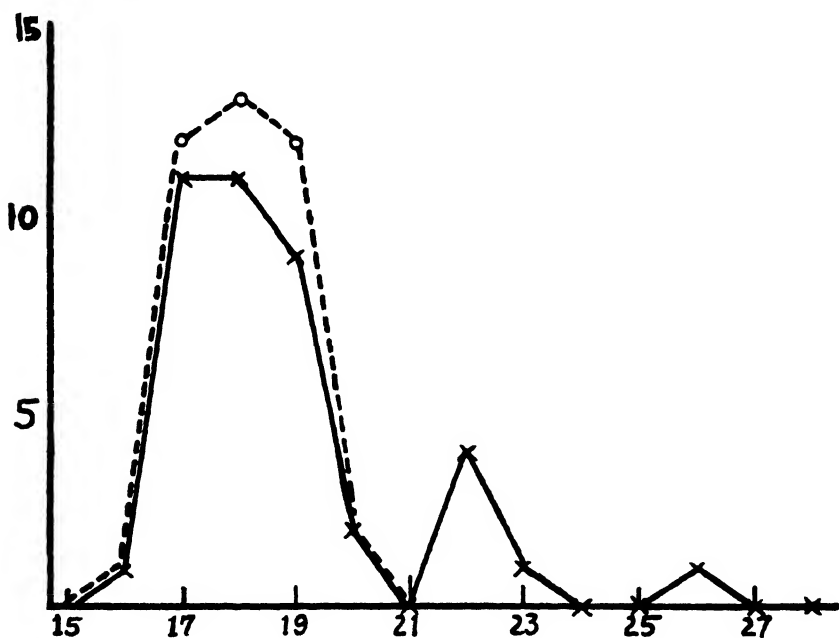


Fig. 18

FIG. 18. Frequency (ordinate) of tomato plants having different numbers of leaves (abscissa) formed before the first inflorescence (crosses and solid line). When the whorled leaves are not counted the broken line and circles give the frequency distribution.

The described abnormalities in phyllotaxis have not been observed below the higher flower clusters in the San Jose Canner tomato.

An experiment was carried out in an ordinary greenhouse to determine whether the presence of a particular leaf or number of leaves was required for flower initiation. In an early stage, when only two fully developed leaves were present on the plants (meaning that the 10th leaf primordium had just been laid down), all leaves were pulled off as soon as they had reached full size, and only a few leaves were left. Whereas this had a pronounced effect

on stem elongation, it hardly affected organ initiation in the growing point and the flower primordium was formed after the 15th–16th node irrespective of the number of leaves and the type of leaves left. This is another indication that flower initiation in the tomato is a “morphological” process, independent of external conditions, and occurs after the growing point has gone through the cycle of leaf initiation for 15–16 times.

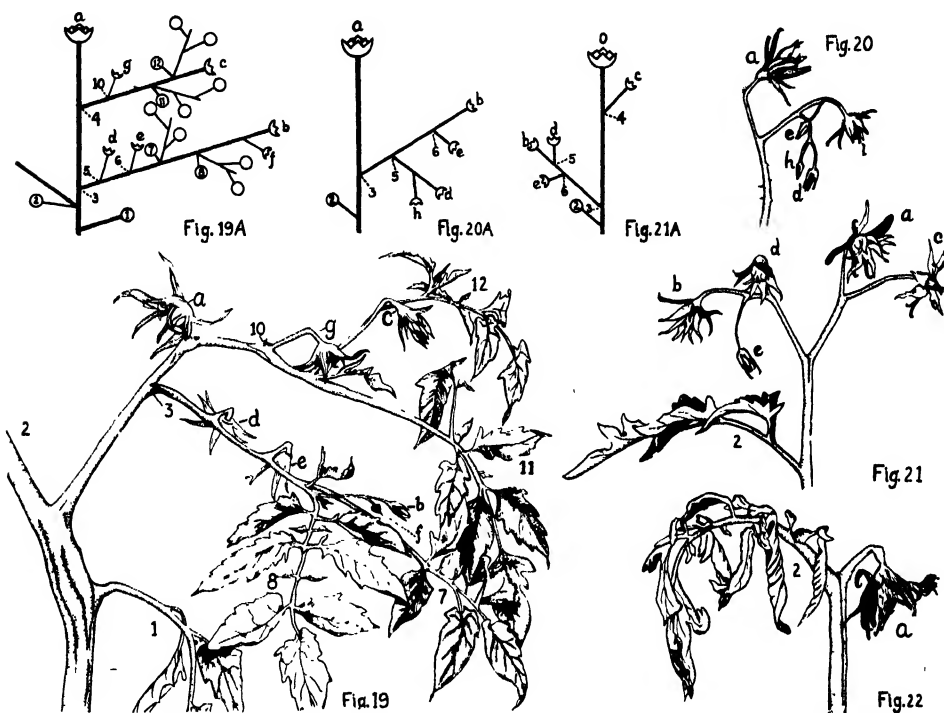
Only one plant was found which did not conform to the above mentioned rules of flower formation and differentiation. Its solitary flower primordium was initiated after the 7th leaf, but nevertheless developed into a normal flower. There were no functional axillary buds in the leaf axils, so that the plant remained 7-leaved. Normal fruit set occurred after anthesis. Only after the fruit started to grow did adventitious buds appear on a small callus formed in the axil of the highest leaf.

Morphology of the Inflorescence. Upon superficial observation the morphology of the tomato inflorescence may seem very complex. It may be a cyme or a simple or branched raceme, leafy or leafless, terminal or seemingly lateral, purely generative or with many vegetative axillary shoots. Various investigators have already explained part of these variations (Crane 1916, Yeager 1927, Bouquet 1931) and including the present observations all can be reduced to the following simple scheme.

After the development of a limited number of leaf primordia the apical meristem broadens and transforms into a flower primordium. This is contrary to Cooper's observation (1927) that the first flower of a cluster forms in the axil of a leaf. If this is the first flower formed on the young plant, sometimes no lateral flowers are present, and a single strongly fasciated flower develops. More often a few of the lower organ primordia on the main axis have become flower primordia (fig. 5). In that case the flower insertion continues the foliar spiral of the shoot, since they are axillary buds in the axils of leaves, which either are still discernible as subtending bracts or are entirely lacking. To complicate the picture these laterals may either be single flowers so that a raceme is formed, or they may develop into 2–3-flowered shoots giving rise to a cyme (figs. 20, 21).

In normal cases the lateral bud of the leaf immediately below the lowest flower primordium is purely vegetative, and after growing out, takes over the main axis of the plant, forming a sympodium. Generally this lateral bud grows up united with the lower portion of the leaf stalk (when pulling a young leaf off the shoot, the lateral bud usually remains attached to the leaf) so that the inflorescence seems to emerge laterally from the shoot, without a trace of a bract (fig. 19). But invariably the leaf opposite the inflorescence does not have an axillary bud, proving that the shoot above this leaf is lateral. There are varietal differences in the number of leaves formed on these lateral shoots before the apex becomes generative again, so that in the

San Jose Canner tomato an inflorescence appears regularly after every fourth or fifth leaf, whereas in other varieties 2 or 3 leaves are formed between inflorescences. This number is independent of the variations in external conditions (nutrition, day and night temperatures, light intensity or duration) as used in present experiments. This was more or less to be ex-



FIGS. 19-22. Tomato flower stands as developed under different night temperatures; day temperature, 26.5° C. All apical flowers (a) are fasciated. Figures 19A-21A are hypothetical reconstructions of the branching of these flower stands. A circle stands for a leaf, a dotted line for a bract, and a half circle for a flower. FIGS. 19 and 19A. Night temperature 26.5° C. Highly vegetative inflorescence. Main shoot terminates in flower a. Leaf 2 and its axillary shoot (which has become main axis) connate. Bracts 3 and 10 and still visible, bracts 4, 5, and 6 are completely absent, and bracts 7, 8, 11, and 12 have grown out into normal leaves. Axillary buds of bracts were transformed into flowers, of leaves remained vegetative. It is possible that flower c instead of flower b terminates the axillary shoot of bract 3, and that the shoot bearing flowers b and f and leaves 7 and 8 is a secondary shoot in the axil of (hypothetical) bract 6. FIGS. 20, 20A, 21, and 21A. Purely generative inflorescences developed in night temperature of 12° C. No trace of subtending bracts can be found. FIG. 22. Night temperature 7° C. Only terminal flower has developed on inflorescence.

pected, since otherwise such characters presumably would not have been recognized by Schlösser (1938) as based on genes.

When the inflorescences develop while the plants are subjected to high night temperatures (20 or 26° C) the lateral shoots below the apical flower pri-

mordium are partly leafy, and terminate in 1-3 flower primordia each (fig. 19). This gives rise to a remarkably complex inflorescence, for in each leaf axil a lateral bud develops bearing some leaves and a terminal flower. This leads to a profusely branched leafy inflorescence, with mostly solitary flowers scattered all through it and seemingly arising laterally from its axis. When the plants are kept at night temperatures of 10° and 5° C, no leaves develop on the inflorescences, which are simple racemes or few-flowered cymes (figs. 20, 21, 22). At intermediate night temperatures (15° C) an intermediate number of leaves grows on the cymes. These temperature effects are evident only many weeks after the plants have been exposed to them, so that transfer of the tomatoes from one to another night temperature treatment does not result in change of the inflorescences already initiated.

Temperature also has an effect on the size of the developed flowers, but low night temperatures or low light intensities do not materially decrease the number of flower primordia initiated per inflorescence. This means that in the tomato the flower initiation is primarily a morphological process in the sense of Sachs (1893), influenced by internal organization and genetic constitution rather than by external factors. Flowering in the tomato is photo-periodically indifferent, as confirmed in the present work.

DISCUSSION

Many of the phenomena described in this paper are abnormalities, or in other words, occur only occasionally. This does not reduce their value for morphological considerations: on the contrary, the author feels that all the observations have given him a much better insight into the normal development of the tomato plant and the potentialities of its meristems. Rischkov (1938) has recently discussed the importance of teratology for morphology and developmental mechanics in plants and concludes: "Teratological phenomena make possible the investigation not only of the prospective potentialities of different plant organs, but also of the phenomena of correlative and autonomous differentiation, of polarization of the meristem, etc."

All described observations of the morphology of the tomato plant not only give a better understanding of its development, but also contribute to morphological concepts. They strongly support the views of Sachs (1893) that we have to distinguish between initiation, determination, elongation, and maturation in the development of an organ. It has been shown that leaves can be initiated either as leaves in a normal 2/5 spiral, or as calyx lobes approximately in a whorl. The second developmental stage, determination, decides the nature of the initiated organ. It was found that neither initiation nor determination is affected by the external conditions which are most important for fruit-set and vegetative development of the tomato. This is exactly what Sachs meant by grouping initiation and determination to-

gether as the morphological stage, when development is ruled by internal forces such as genetic constitution, and is rather independent of changes in the external conditions. The elongation and maturation on the other hand (Sachs' physiological stage) is almost entirely dependent on the prevailing conditions of the surroundings, especially night temperature (Went 1943). In addition we have to distinguish between the vegetative growing point and the flower meristem into which it is transformed after the first 13-17 leaves have been initiated. No external conditions were found to influence this transformation. In fully developed plants the transformation of the apical meristem and of the higher laterals occurs regularly after initiation of 4 or 5 leaves, but in young plants 13 or more foliage leaves must have been initiated before a flower can fully develop. In exceptional cases the transformation may take place earlier in the life of the tomato plant, but then initiation and determination of the flower-parts is defective and does not proceed beyond an early stage of development. Independently of the poor organ development the generative meristem widens and enlarges proportionally to the number of previously initiated leaves. It almost seems as if the plant continuously forms a limited amount of material required for the formation of a flower meristem. This usually is released for the first time after the 13th-17th leaf, and is then in such excess that a fasciated flower results. Completely independent of the materials for flower meristem formation are the determination factors for the different flower-parts. They become available in sufficient amounts only after the 13th-17th leaf. Earlier the calyx primordia only develop, with the aid of leaf growth factors, into seemingly normal leaves, but although a large flower meristem is present and organ primordia are initiated, they do not develop into petals and stamens.

The observations also strongly support the view of Grégoire (1938) on the nature of the flower. No facts were found which support the idea that the tomato flower is a foreshortened vegetative shoot. On the contrary, phyllotaxis is not continuous from normal foliage leaves to leaves transformed from calyx lobes. The meristem of the flower is radically different from the vegetative growing point: whereas the latter very seldom broadens into a fasciation, and rarely widens enough to cause the stem to branch dichotomously, the first flower primordium is invariably fasciated. But notwithstanding the great plasticity of the flower meristem no reversion to a vegetative meristem was ever observed in these tomatoes.

In view of these facts it seems desirable to extend Sachs' scheme of growth of the stem and its derivative organs as follows:

- A. Meristematic or morphological stages. Growth mainly by cell division; largely independent of external conditions. (Some exceptions to this rule are noted.)

1. *Transformation*. Meristem as a whole is vegetative or transforms into a flower primordium. In a number of plants this transformation is affected by length of day.
 2. *Initiation*. Number and place of organs is established. Blaauw *et al.* (1932) showed that in the tulip flower temperature affects the number of flower parts initiated.
 3. *Determination*. Nature of initiated organ becomes established. Differentiation of tissues starts. Organ attains its essential form. May be influenced by level of nutrition (De Vries 1903).
 - 3 *bis*. *Dedifferentiation*. Differentiated cells become meristematic again and may give rise to any structure. Occurs in case of regeneration of new organs on old ones. In many instances high auxin concentrations cause dedifferentiation.
- B. Physiological stages, easily influenced by external conditions.
4. *Elongation*. Increase of embryonic organ to final size, mainly through cell enlargement.
 5. *Maturation*. Final chemical changes in the full grown cells and tissues.

In the described tomatoes all stages of fasciation as summarized by Schoute (1936) were observed: typical fasciation both in vegetative and generative meristems, and radiate and ring meristems in flowers. In addition spiral fasciation was observed in a flower primordium, comparable with biastrepis in stems. On the other hand no connations in stems were found. The typical fasciation is present in a very modest degree in vegetative stems, and there usually leads to dichotomy. In most cases the foliar spiral has started to show abnormalities some nodes below the dichotomy, and then no conclusion can be reached as to the relation of the direction of the foliar spiral in the two branches to the original direction. In some of these cases the two branches had opposite spirals. But in two stems where dichotomy occurred practically without previous phyllotactical disturbance, both branches followed the original direction of the foliar spiral.

Tricotyledonous plants are interesting in connection with fasciation. We have to assume that such a condition arises through enlargement of the growing point, so that three instead of two cotyledons can be initiated simultaneously in a whorl. This enlarged growing point persists for a shorter or longer period afterward, so that the first leaves also form in a whorl of three. Then either the size of the growing point decreases again to normal and a $\frac{2}{5}$ phyllotaxis appears, or the whorled condition persists until the enlarged growing point splits in two and true dichotomy results. In most other cases (except fig. 15) dichotomy is preceded by an increased number of leaves in the foliar spiral, decreasing the divergence to well below 120° . This also indicates enlargement of the growing point previous to the actual bifurcation.

SUMMARY

The more important abnormalities observed in the development of the tomato plant are as follows:

Anomalous phyllotaxis occurs in 5-20 per cent of the plants just below the first inflorescence. The upper 3-7 leaves are supernumerary and appear more or less whorled. Since all intermediate stages between a normal calyx primordium and a normal leaf complete with axillary bud have been found, it is concluded that these upper whorled leaves are transformed calyx primordia.

Flower primordia develop into normal flowers only after the 14th-17th foliage leaf. Flower primordia initiated before so many leaves are formed remain arrested in early stages of development and differentiation, but enlarge to some extent. In this way models of flower primordia are produced, which clarify a number of problems connected with flower initiation.

The influence of temperature on some of these morphogenetic processes is described.

Various forms of fasciation, especially in flower primordia, are observed and described.

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PECULIAR FERN PROTHALLIA

W. N. STEIL

INTRODUCTION

In several cultures of gametophytes of a species of *Tectaria*,¹ the spores of which were obtained from the Botanical Garden of Leiden, Holland, April 20, 1935, there appeared a number of peculiar gametophytes of another fern, undoubtedly of a *Dryopteris* species. Young sporophytes produced by the gametophytes of the fern were typically those of *Dryopteris*. In a number of other cultures made later from sowings of spores obtained from the same Botanical Garden, the observations herein described have been confirmed.

The cultural conditions under which the gametophytes were grown have been described by the author (1919).

THE VARIEGATED GAMETOPHYTE

The prothallia were examined from time to time, but showed no peculiarities until they became quite large and heart-shaped, when definite regions of different degrees of intensity of color, varying from green to white, made their appearance. Several well defined regions of this nature are shown in a photomicrograph (fig. 1) of the anterior portion of a prothallium. Just posterior to the apical notch is represented a triangular light green region almost completely surrounded by a nearly albinic one. Other portions of the prothallium are also characterized by nearly albinic cells. When the cells of the regions of the gametophyte, which appeared almost white, were examined under the microscope, it was readily observed that they contained fewer and smaller as well as paler plastids than the ordinary cells of the prothallium. The walls of these cells are also thinner than those of the darker green cells (fig. 1). The outer portions of the lobes of the gametophyte are composed, to a considerable extent, of cells which contain so many ordinary chloroplasts that the cells appear black in the photomicrograph. A variegated secondary gametophyte with several nearly albinic portions is represented by figure 2. A gametophyte originating from one of the lobes of the secondary gametophyte possesses only green cells.

In some of the gametophytes, no such definite regions varying in intensity of color as described above are present. Instead, the chlorophyllose and the nearly albinic regions are composed of smaller or larger groups of cells (figs. 3, 4, 6).

¹ Labeled *Dryopteris trifoliatum*. It has been impossible to obtain fronds of the fern for positive identification.

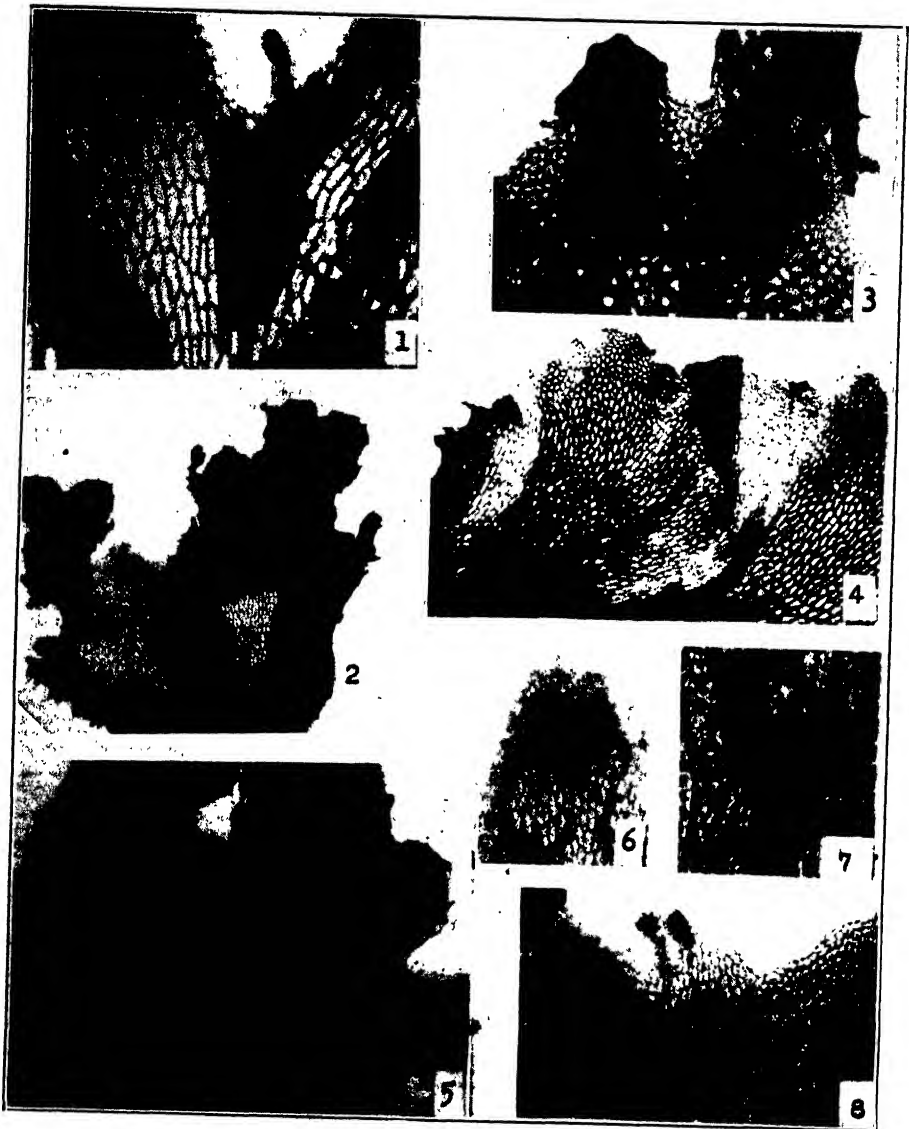


FIG. 1. A variegated gametophyte showing a pale green wedge-shaped portion in the region of the apical notch. This region is almost surrounded by a nearly white portion. The gametophyte also shows a short sporangium-like outgrowth from the apical region. $\times 35$. FIG. 2. A photomicrograph of a secondary gametophyte. Several nearly albinic portions are shown in the figure. $\times 35$. FIG. 3. A photomicrograph of a small portion of a gametophyte showing the nearly white and the dark-green portion. $\times 40$. FIG. 4. A photomicrograph of a small portion of a gametophyte which shows clearly the variegation. $\times 25$. FIG. 5. A photomicrograph of a large gametophyte bearing sex-organs on both surfaces. Numerous archegonial projections and secondary antheridia were also formed on both surfaces. $\times 20$. FIG. 6. A photomicrograph of a portion of a variegated

These regions of the gametophyte just described were generally quite common, especially in the apical portion, and also occasionally in the posterior region of the prothallium.

The majority of the primary and the secondary gametophytes (fig. 2) were characterized by definite regions varying from dark green to nearly white.

The regions of triangular form originate, no doubt, from segments of the apical cell. When the apical cell divides, it loses chloroplasts to its adjacent segments on either side. Hence, further divisions of the segments may result in a nearly white or a pale green region as the apical cell continues to divide. If, at an early stage in divisions of the segments, the chloroplasts continue to multiply, other zones outside of the original triangular region may be produced.

The regions of white or pale green in other portions of the gametophyte cannot be accounted for in the manner described. The formation of lighter and darker regions involve, no doubt, ordinary cells of the gametophyte. Since such cells retain their power to divide for only a short time, the regions of pale green or nearly white are much limited in size. These gametophytes are similar to those first described by Andersson (1923) in *Adiantum cuneatum*, and later in other species of ferns by Andersson-Kottö (1930, 1931) who made a detailed study of such gametophytes in several ferns and showed that the variegation is hereditary.

The peculiar gametophytes described by the author, no doubt, also owe their nature to hereditary factors and not to a virus or to cultural conditions under which the gametophytes were grown.

SEX-ORGANS

The prothallia of the cultures when examined on July 5, 1935, had grown to a large size and bore antheridia and archegonia on both ventral and dorsal sides. Since the gametophytes were grown in Erlenmeyer flasks placed on a glass plate, which admitted light also from below, the illumination of the two surfaces of the gametophyte was nearly equal. Hence, the development of the sex-organs on the two surfaces was due to an environmental condition. In the second set of cultures, made at a later time, the prothallia were illuminated only on the upper side and were then observed to produce sex-organs and rhizoids on only the ventral side.

The cushion of the older prothallia frequently appeared to be of unusual thickness and it produced a large number of "archegonial projections"

gametophyte showing a thickened process produced as an outgrowth of the apical notch. $\times 25$. FIG. 7. A photomicrograph of a portion of a gametophyte with tracheids a short distance back of the apical notch. $\times 120$. FIG. 8. A photomicrograph of a gametophyte with sporangia-like structures produced in the sinus region of the gametophyte. $\times 25$.

Stated magnifications are approximate. The author is indebted to Professor F. A. Bautsch, S.J., for the photomicrographs.

(fig. 5) similar to those described by Heim (1896) in *Doodya caudata*. Secondary prothallia in large numbers were formed from these archegonial projections. The antheridia at an early stage in their development often produced secondary prothallia. Frequently antheridia originated from the lid cell, or a ring cell of the antheridium. Sometimes the single initial cell of an antheridium was observed to form a short filament which produced a prothallium. The formation of secondary antheridia from the lid cell or from one of the ring cells of the antheridium was of common occurrence. The formation of these secondary prothallia and secondary antheridia are similar to those described by Steil (1921) in *Polypodium irioides*.



FIG. 9. A photomicrograph of a variegated gametophyte of a *Dryopteris* species. $\times 40$ (approx.).

APOGAMY

Usually a lobe was produced in the sinus region of a gametophyte which had grown to large size (figs. 6, 7). The prothallium occasionally formed a plate of cells or a cylindrical outgrowth from the apical notch similar to that described by Farlow (1874), and Steil (1918, 1919, 1933, 1939) and others in gametophytes of apogamous ferns. Tracheids could be readily observed in the gametophyte, usually a short distance from the apical notch (figs. 7, 8, 9). Frequently outgrowths enlarged at their distal ends

were produced in the apical notch (figs. 1, 8). The enlarged portion, nearly spherical in form, was composed of a definite layer of outer cells and of inner cells of large size and nearly spherical in form. These structures, no doubt, were sporangia, each containing cells resembling spore mother cells. Similar non-functional sporangia originating from the gametophytes of the fern have been described by Lang (1898, 1929). It is obvious that sporangia of this nature, although abortive, are of apogamous origin.

SUMMARY

1. The gametophyte of a fern, undoubtedly of a *Dryopteris* species, is described.
2. A large proportion of the gametophytes were variegated. The trait is of a hereditary nature.
3. The gametophyte, typically heart-shaped, of large size, and bearing numerous hairs, produced antheridia and archegonia in large numbers.
4. The antheridia produced gametophytes and secondary antheridia.
5. The archegonia produced from their neck cells normal gametophytes and antheridia.
6. Archegonia frequently formed "archegonial projections" which finally produced heart-shaped prothallia, resembling in all respects the primary ones.
7. Antheridia, archegonia and rhizoids in one set of cultures were formed on both surfaces of the gametophyte.
8. The gametophyte, so far as could be determined, always produced the embryo apogamously.
9. Sporangia-like structures were occasionally formed from the sinus of the gametophyte.

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INDEX TO AMERICAN BOTANICAL LITERATURE

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Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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(including anatomy, and cytology in part)

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**BACTERIOSTATIC AND BACTERICIDAL PROPERTIES OF
ANTIBIOTIC SUBSTANCES, WITH SPECIAL REFER-
ENCE TO PLANT-PATHOGENIC BACTERIA¹**

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INTRODUCTION

The ability of certain microorganisms to inhibit the growth of various bacteria and fungi is due largely to the production of specific agents, designated as antibiotic substances, that possess bacteriostatic or fungistatic properties (9). The bactericidal and fungicidal activities of these substances are not as pronounced, thus distinguishing them from the common chemical antiseptics and germicides.

Both the organisms producing antibiotic substances and the substances themselves are selective in their action upon bacteria and fungi, affecting some species and not others even sometimes in the same genera. These differences in activity are largely quantitative, but they may also be qualitative in nature. Most of the substances so far isolated act primarily upon gram-positive bacteria and only to a limited extent or in much higher concentrations upon gram-negative organisms; other substances, however, act selectively upon some bacteria found within each of these groups. Similar differences are also observed in the action of antibiotic substances upon the fungi. This differential action of a substance upon a number of bacteria is designated as the "antibiotic" or "bacteriostatic spectrum"; each antibiotic substance is characterized by a specific spectrum. When two substances of unknown nature and of different origin have the same spectrum, one is led to assume that they are the same chemically or at least closely related.

The effect of antagonistic microorganisms and antibiotic substances upon plant pathogens has been largely limited to the fungi (3, 4, 5, 9, 19), plant-pathogenic bacteria having been given but scant consideration. The bacterial pathogen was often found to produce a substance bringing about its own inhibition, for example *Pseudomonas destructans*, the cause of turnip rot (6). Other antibiotic agents are produced by soil saprophytes, as certain soil bacteria active against *Ps. citri* (2). Solnzeva (8) demonstrated that myxobacteria are capable of bringing about the lysis of various plant-pathogenic bacteria; a thermostable lytic substance was produced which was not studied further, however.

The ecological relationships of plant pathogenic microorganisms are different in many respects from those of animal pathogens. This is because

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the plant pathogens usually are not transmitted directly from one infected individual to another, but largely through an intermediate agency, such as infected seed, wind carried spores, animals, and the soil. The plant pathogen thus often comes in contact with other microorganisms that may exert antagonistic effects upon it, thereby modifying its survival. This is especially true of the soil, where antagonistic microorganisms have an opportunity to grow and produce antibiotic substances, whereby the growth of the pathogen is inhibited or even destroyed. The survival of plant-pathogenic microorganisms in the soil, as influenced by antagonistic microorganisms as well as by antibiotic substances, is of considerable theoretical and practical importance.

No attempt was made to carry out detailed investigations of the effect of a large variety of antibiotic substances upon plant pathogens as a whole or even upon various plant-pathogenic bacteria. A study has been made, however, of the activity of a few substances upon a few bacteria in order to throw some light upon this highly significant natural phenomenon. This is particularly significant since most of the organisms producing these substances are inhabitants of soils or composts. In connection with two comprehensive surveys on the production of antibiotic substances by fungi and actinomycetes (13, 15), several antibiotic agents were isolated. A comparative study was then made (14, 16, 17, 18) of the effect of these agents upon various bacteria comprising both saprophytic forms and human and animal pathogens. The following investigation of the action of some antibiotic substances upon certain bacteria causing plant diseases makes possible broad generalizations concerning the activity of these substances upon bacteria as a whole and upon plant pathogens in particular as compared with saprophytes and animal pathogens.

FORMATION AND NATURE OF ANTIBIOTIC SUBSTANCES

Although the ability to produce antibiotic substances may be characteristic of certain groups of microorganisms and especially of certain genera, only a given species within a genus or even a given strain may be utilized. This is due to the fact that the particular strain may produce the antibiotic substance in sufficient concentration to justify its isolation. Specific strains may be more active under certain conditions of growth and other strains under others (12). Among the fungi, for example, the genera *Penicillium*, *Aspergillus* and *Trichoderma* contain many species that are capable of producing, under certain conditions of nutrition and environment, one or more antibiotic substances. Some microorganisms, like certain yeasts, were found to produce antibiotic agents only in the presence of the antagonized organism. Some of the larger groups of fungi, especially the Phycomycetes and Basidiomycetes, have so far been found to contain only very few forms that have the capacity of producing antibiotic substances.

A fairly large number of antibiotic substances has already been isolated from cultures of different microorganisms. Many of these have been concentrated, but only a few have been crystallized. These substances vary greatly in chemical nature, in mode of action upon bacteria and fungi, in toxicity to animals and in their activity *in vivo*. Some organisms produce more than one antibiotic substance: *Penicillium notatum* forms penicillin and notatin; *Aspergillus flavus*, aspergillic acid and flavicin; *A. fumigatus*, spinulosin, fumigatin and fumigacin; *Actinomyces antibioticus*, actinomycin A and B. Different organisms may also produce the same type of antibiotic substance. Penicillin, for example, was found to be formed not only by strains of *P. notatum* and *P. chrysogenum* but also by *A. flavus* (10). It is still impossible to say definitely how general this phenomenon is, but it is

TABLE 1. *Bacteriostatic spectra of four antibiotic substances.*

Activity, dilution units, thousands per gram

Test organism	Gram stain	Penicillin ^a	Actinomycin ^b	Streptothricin ^c	Clavacin ^d
<i>Staphylococcus aureus</i>	+	9,500*	20,000	200	100
<i>S. aureus</i>	+	1,000†
<i>Sarcina lutea</i>	+	38,000*	60,000	100	500
<i>Bacillus subtilis</i>	+	19,000*	60,000	750	200
<i>B. megatherium</i>	+	1,900*	40,000	200	100
<i>B. mycoides</i>	+	5*	40,000	< 3	200
<i>Clostridium welchii</i>	+	1,500†	1,000
<i>Actinomyces</i> sp.	+	1,000†	10	10-50
<i>Neisseria</i> sp.	-	2,000†	20
<i>Brucella abortus</i>	-	2†	10	100
<i>Shigella gallinarum</i>	-	2†	20	300
<i>Pasteurella</i> sp.	-	1†	< 10	100
<i>Listerella monocytogenes</i>	-	300	18
<i>Hemophilus</i> sp.	-	50	30
<i>Salmonella schottmülleri</i>	-	< 1†	< 10	200	60
<i>S. aertrycke</i>	-	10*
<i>Pseudomonas fluorescens</i>	-	< 5*	10	< 3	6
<i>Serratia marcescens</i>	-	< 1	< 5	5	60
<i>Aerobacter aerogenes</i>	-	< 5*	< 5	30	50
<i>Escherichia coli</i>	-	< 1†
<i>E. coli</i>	-	< 5*	5	100	100

^a Our own data based on a sample of penicillin having 470 Oxford units are marked *; data reported by Abraham *et al.* (1), based on a less active preparation, are marked †.

^b Based on data reported elsewhere (17).

^c Based on data reported elsewhere (18).

^d Based on data reported elsewhere (14). Much of the above data has been rechecked with fresh preparations.

safe to conclude that antibiotic substances comprise a great variety of chemical compounds, some of which may be formed by more than one organism.

The mode of action of antibiotic substances upon bacteria also varies considerably. Such substances usually interfere with microbial cell division; some affect the metabolic or respiratory processes of the cell; others function as enzymes or interfere with certain enzymatic reactions (10).

The bacteriostatic spectra of four typical antibiotic substances are shown in table 1. Highly concentrated preparations were used, which differed greatly in the degree of purification. Penicillin acts primarily upon gram-positive bacteria and only upon very few gram-negative organisms; however, whereas *Bacillus mycoides*, a gram-positive organism, is only little affected by this substance, *Neisseria* and certain other gram-negative bacteria are sensitive to it. Actinomycin also acts largely upon gram-positive bacteria, with a more gradual transition in the degree of sensitivity between the different groups of bacteria, the cocci and aerobic spore-formers being at one extreme, and *Escherichia*, *Serratia*, and *Pseudomonas* groups at the other. Streptothricin acts upon certain gram-positive and gram-negative bacteria though some organisms within these two groups are only little affected by this substance; there is no important difference in the degree of sensitivity to streptothricin by the gram-positive and the gram-negative bacteria. Clavacin acts nearly alike upon all the bacteria so far tested, with only quantitative differences in the degree of sensitivity of the different organisms; it is also highly active against certain fungi (11). The four antibiotic substances selected at random for this study are thus found to differ greatly in their antibiotic spectra. This justifies the conclusion that the mode of action of each of these substances upon bacteria is different. It may be of interest to recall further that penicillin and streptothricin show only little toxicity to animals, whereas actinomycin and clavacin are highly toxic (7).

NATURE OF ANTIBIOTIC SUBSTANCES USED IN THESE INVESTIGATIONS

Seven antibiotic agents were selected for the following investigations. They were isolated from different organisms naturally occurring in soils or in composts. These organisms were grown upon different media, the nature of the medium and the conditions of growth depending upon the organism, its metabolism, and the environment most favorable to the production of the antibiotic substance. Some substances are produced in synthetic media, others in complex organic media. Some of the organisms were grown in stationary liquid cultures and others in submerged and agitated cultures; some in liquid media and others in semi-solid agar media. Five of the substances were obtained from fungi and two from actinomycetes. The substances used varied greatly in the degree of purification, some being highly

purified and concentrated, and others being crude preparations isolated from the medium and only partly purified.

The nature and potency of these substances can be briefly summarized as follows:

1. *Penicillin*. The preparation used in these experiments was isolated from a culture of *P. notatum*. It was highly concentrated, having 470 Oxford units with *B. subtilis* as the test organism.

2. *Clavacin*. This was a crude and not highly purified preparation isolated from cultures of *A. clavatus* (14).

3. *Fumigacin*. This substance is produced by *A. fumigatus*. Although it has already been crystallized, only a crude preparation was used here. Fumigacin is not readily soluble in water, is active largely against gram-positive bacteria, and is characterized by limited toxicity to animals (14).

4. *Flavicin*. This substance is produced by *A. flavus* and is comparable in its properties to penicillin. A crude preparation containing also a small amount of aspergillic acid was used (12).

5. *Chaetomin*. This material was isolated from an antagonistic strain of species of *Chaetomium* (20). It is characterized by an activity largely directed against gram-positive bacteria, but possesses certain chemical and biological properties that make it quite distinct from penicillin or flavicin, such as high activity against *B. mycoides*.

6. *Actinomycein*. This was a highly purified preparation of Actinomycein A, produced by *Act. antibioticus*. It had an activity of about 10,000,000 *B. subtilis* units (16).

7. *Streptothricin*. Both crude and purified preparations of this material, produced by *Act. lavendulae* (18), were used.

A detailed study of the selective antibiotic action of some of these substances as compared with chemical antiseptics has been published (17).

METHODS

Methods of Testing Bacteriostatic Action. A number of methods are used for measuring the activity of antibiotic substances. They are based largely upon the inhibition of growth and multiplication of specific test bacteria; some of the methods are based upon interference with a physiological reaction of the test organism. The bacteria that are commonly used as test organisms comprise *S. aureus*, *B. subtilis*, *Micrococcus* sp., and *E. coli*. The following three methods are employed in making the tests: (a) the streak-plate method, in which several test organisms, differing in the degree of their sensitivity to the antibiotic substances, are used simultaneously; (b) the agar diffusion or cup method, where one test organism is used, usually *B. subtilis* or *S. aureus*; (c) the dilution culture method with only one test organism. The last method was found to be least suitable for this

study. The first has the advantage that the sensitivity of several organisms can be measured on the same plate with different dilutions of the antibiotic substance. The second has the advantage of giving more accurate quantitative results for practical purposes.

The units of measurement reported for the plate method are based upon the dilution of the substance. The minimum concentration of the active material that inhibits growth of the test organism is taken as the end point. The ratio between the volume of medium and the concentration of the active material that is required to bring about inhibition of the growth of the test organism represents the activity units. The zone of inhibition produced on

TABLE 2. *Bacteriostatic action of three antibiotic substances, as measured by two different methods.*

Nature of substances	Purity	Agar-streak method ^a	Agar diffusion (cup method ^a)	
			Dilution ^b	Inhibition zone, mm. ^c
Penicillin	Highly purified material	units 19,000,000	1: 470,000	22.0
Penicillin	Crude culture filtrate	1,000	1: 25	23.4
Flavicin	Purified	45,000	1: 600	22.0
Flavicin	Crude filtrate	100	Undiluted	23.0
Streptothricin	Purified	750,000	1: 2,000	26.7
Streptothricin	Crude filtrate	300	1: 2	25.5

^a *B. subtilis* used as test organism in both cases.

^b On basis of 1 gm. or 1 ml. of material.

^c Diameter of cup itself - 8 mm.

the plate, expressed in millimeters, is used as a unit of measurement for the cup method. Only for penicillin and streptothricin were standards available; the other substances could be compared against these standards, with one important reservation, namely, that the rates of diffusion of various materials differ; hence no single standard can be employed for comparing the activity of different antibiotic substances.

Ordinary glucose-free nutrient agar media, suitable for the growth of the test organisms were used. The plates were incubated at 30° C for 18-24 hours. The results obtained by the two methods and based upon the use of 3 purified and 3 crude preparations are given in table 2. On the basis of these results, one is justified in concluding that both methods are comparable.

Methods of Testing. Bactericidal Action. Several methods are commonly utilized for measuring the bactericidal action of antiseptics and disinfectants. They differ in the nature of the test organism, culture medium or bacterial suspension, and time and temperature of incubation. These methods can be applied with certain modifications to antibiotic substances. However, since these agents are primarily bacteriostatic in nature, whereas their bactericidal action requires a much longer period of time than the ordinary chemical germicidal agents, this phase of the problem was given only limited consideration. A single simple procedure was used as described later.

Strain Variation. Before any generalization can be made concerning the sensitivity of a certain bacterial species to an antibiotic substance, it is essential to establish the variation in sensitivity of different strains within the given species. This becomes particularly significant when one recognizes two well established facts: first, different strains of a bacterial species, difficult to distinguish microscopically, culturally, and physiologically, may show marked variations in the degree of their sensitivity to a given antibiotic substance; second, test organisms may gradually become more resistant to a substance on continuous passage through media containing increasing concentrations of this substance. Certain data pertaining to the sensitivity of different strains of three common spore-forming bacteria to three antibiotic substances are presented in table 3.

The three spore-formers are sensitive alike to clavacin and to fumigacin. The differences in sensitivity obtained for the various strains of each species are greater than between the three different organisms. For example, the average activity of clavacin against *B. subtilis* is 47,000 with variations of 10,000 to 100,000; against *B. mycoides* 39,000 (10,000–75,000); and against *B. cereus*, 17,000 (10,000–25,000). Similar results were obtained for fumigacin. The variation of the sensitivity of the different strains of *S. aureus* against the bacteriostatic action of these two substances was also found to be quantitative rather than qualitative in nature (14). The most striking differences, however, are obtained for streptothricin. *B. subtilis* is highly sensitive and *B. mycoides* is very resistant to this substance, as brought out elsewhere (18). The results presented here show, however, that when several strains of the same organism are used, certain variations are obtained that tend to throw doubt upon the significance of these differences. There were two peculiar exceptions for *B. subtilis*, namely, Nos. 243 and 970.

The sample of streptothricin used in these tests gave for seven strains of *B. subtilis* (except Nos. 243 and 970) a variation of 7,500 to > 33,000 units, with an average of 23,800 units or more; for eight strains of *B. mycoides*, the variation was from < 330 to 5,000, with an average of 2,330 units or

less; for seven strains of *B. cereus*, the variation was from < 300 to 10,000, with an average of 5,000 units or less. It is interesting to note that *B. cereus* overlaps in the degree of its sensitivity to streptothricin the two other spore-forming bacteria, coming much nearer to *B. mycoides*, however. Dr. N. R. Smith, who kindly supplied these cultures, is of the opinion that *B. mycoides* is to be considered as a variety of *B. cereus*. This is well borne out by the results presented here. Of the two exceptional strains of *B. subtilis* that

TABLE 3. *Strain variation among spore-forming bacteria in their sensitivity to antibiotic substances.*

Activity, dilution units, thousands per gram

Organism	Strain No.	Streptothricin	Clavacin	Fumigacin
<i>B. subtilis</i>	0	> 33.0	100	75
"	6	25.0	50	50
"	231	> 33.0	100	50
"	243	< 3.3	50	< 10
"	968	20.0	25	33
"	969	> 33.0	50	75
"	970	< 3.3	20	100
"	971	7.5	20	10
"	972	15.0	10	20
<i>B. mycoides</i>	0	< 0.3	20	10
"	233	2.5	75	100
"	306	2.5	25	50
"	317	2.5	10	50
"	318	0.8	75	15
"	319	2.0	30	20
"	911	5.0	50	15
"	912	3.0	30	10
<i>B. cereus</i>	0	< 0.3		
"	201	2.0	10	< 10
"	202	10.0	15	30
"	203	7.5	15	50
"	305	5.0	15	75
"	830	5.0	20	30
"	847	5.0	25	75

showed low activity to streptothricin, one, No. 970, proved to be the so-called Michigan strain, which should really be called *B. cereus*. The other questionable *B. subtilis* strain (No. 243) that gave 2,500 units may either represent an exception from the average or it may be another special case, not as yet recognized.

Although these results are sufficient to emphasize the danger of generalizations concerning the sensitivity of a given organism to an antibiotic substance based upon the testing of a single strain of an organism, it can still indicate broadly the selective action of the substance upon a particular bacterial species.

BACTERIOSTATIC ACTION OF ANTIBIOTIC SUBSTANCES AGAINST PLANT
PATHOGENIC AND SAPROPHYTIC BACTERIA

In this study, 9 plant-pathogenic bacteria, 2 saprophytes, and 2 animal pathogens were compared. These bacteria and their gram reaction are listed as follows:

Organism	Gram stain	Organism	Gram stain
<i>Ph. tumefaciens</i>	—	<i>Ph. michiganensis</i>	+
<i>Ph. campestris</i>	—	<i>Ph. pruni</i>	—
<i>Ph. phaseoli</i>	—	<i>E. coli</i>	—
<i>Ph. glycinea</i>	—	<i>S. aureus</i>	+
<i>Ph. syringae</i>	—	<i>B. subtilis</i>	+
<i>Ph. solanacearum</i>	—	<i>S. lutea</i>	+
<i>Ph. stewartii</i>	—		

Table 4 shows the sensitivity of these bacteria to six of the antibiotic substances, as determined by the agar-streak dilution and the agar-cup diffusion methods. Some of the tests, as for *E. coli* and *B. subtilis*, were repeated many times, whereas others were made only two or three times. It is quite possible that other strains of the same organisms may give somewhat different results.

Actinomycin, with a general high activity against gram-positive bacteria (*B. subtilis* and *S. aureus*) and a limited activity against the gram-negative organisms of the *Aerobacter* and *Escherichia* (*E. coli*) groups, has a marked selective action upon the gram-negative plant pathogens, some of which are very sensitive and others very resistant. The important point to note is that these bacteria do not behave as a group. The gram-negative *P. glycinea* is as sensitive to this substance as the gram-positive *P. michiganensis*, whereas *P. stewartii* is as resistant as *E. coli*. On the other hand, clavacin, which does not show any marked specific differences in activity against gram-positive and gram-negative bacteria in general, shows little difference against the various plant pathogens.

Streptothricin has been found to have a selective action upon bacteria within each group rather than between the two groups as distinguished by their staining reactions. Its action on the plant-pathogenic bacteria proved to be quantitative rather than qualitative, the range of activity varying from 5,000 units for *P. solanacearum* to 150,000 for *P. tumefaciens*. Fumigacin and chaetomin, active largely against gram-positive bacteria and not against *E. coli*, showed considerable activity against some of the plant pathogens and comparatively little activity against others, both within the group of gram-negative bacteria.

Penicillin is known to have little if any activity against most of the gram-negative bacteria. Although some of the plant pathogens showed a certain degree of sensitivity to this substance, this was so limited that even the sen-

sitive cultures (*P. tumefaciens* and *P. phaseoli*) may be considered as fairly resistant when compared with the sensitivity to penicillin of the gram-positive bacteria (*S. aureus*, *B. subtilis*).

The results obtained by the agar diffusion method show that the plant-pathogenic bacteria fell midway between *E. coli* and the two gram-positive bacteria. There was considerable variation, however, in the degree of resistance of the different bacteria, some being more and others less sensitive. It is to be recalled, in this connection, that gram-negative animal-pathogenic bacteria, such as *Brucella*, *Pasteurella*, and especially *Neisseria* and *Hemophilus*, are far more sensitive to the known antibiotic substances than are the gram-negative bacteria belonging to the *Escherichia*, *Aerobacter*, *Serratia*, and *Pseudomonas* groups.

One may thus conclude that the plant pathogenic bacteria do not behave as a group as regards their sensitivity to antibiotic substances. Despite the fact that most of them are gram-negative, some are more sensitive to certain agents and others more resistant, depending on the nature of the agent as well as of the organism. As a group, however, the plant-pathogenic bacteria of the gram-negative type are similar to the many animal pathogens of the same type, being more resistant than the gram-positive bacteria and less resistant than the gram-negative bacteria of the *Escherichia* type.

Since the substances studied here are not known chemically, their activity cannot be compared on a molar basis. The very fact that they were of different degrees of purity makes it impossible even to compare them on a gram basis. The best that can be done, therefore, is to compare them largely on the basis of their selective activity upon the various bacteria and only very roughly on a weight basis.

BACTERICIDAL EFFECTS OF ANTIBIOTIC SUBSTANCES

The bactericidal action of the antibiotic substances was tested against three different bacteria, namely, *E. coli*, *S. aureus*, and *P. tumefaciens*. The organisms were grown in nutrient broth for 24 hours at 37° C. One-half-milliliter portions of the cultures were then added to 9.5-milliliter portions of sterile tap water and the antibiotic substances added in dilutions varying from 1:10,000 to 1:100,000. The treated cultures were now incubated at 37° C, and plated after 20 and 40 hours' incubation, nutrient agar being used. The plates were also incubated at 37° C, for 24-48 hours, and the total number of colonies was counted. The counts represent the number of viable and reproducible cells left in each culture. The results are presented in table 5.

Actinomycin, which has only comparatively little bacteriostatic action against *E. coli*, has also limited bactericidal action; even a dilution of 1:10,000 was not sufficient to sterilize the culture completely in 40 hours.

although the number of cells was reduced by about 80 per cent. The same was true of penicillin. Thus both substances, which are characterized by a limited bacteriostatic effect against *E. coli*, have also limited bactericidal action upon this organism. Streptothricin, an agent strongly bacteriostatic against *E. coli*, is also strongly bactericidal; a dilution of 1:100,000 was sufficient nearly to sterilize the culture in 20 hours and completely to sterilize it in 40 hours. The same is true of clavacin, another agent highly active against gram-negative bacteria; however, a larger concentration of this sub-

TABLE 5. *Bactericidal action of antibiotic substances.*
Thousands of bacteria in 1 ml. of diluted culture

Antibiotic substance	Concen- tration, mgs./10 ml.	Test organism					
		<i>E. coli</i> ^a		<i>S. aureus</i> ^b		<i>P. tumefaciens</i> ^c	
		Incubation hours					
		20	40	20	40	40	
Control		140,000	218,000	36,000	252,000	1,020	
Actinomycin	1.0	27,700	39,500	< 0.1	< 0.01	< 0.01	
Actinomycin	0.1	76,400	111,000	26	2	1.6	
Streptothricin	1.0	0.1	< 0.01	1	2	1.8	
Streptothricin	0.1	3.0	< 0.01	50	32	3.4	
Penicillin	0.5	25,300	26,300	124	69	1.4	
Penicillin	0.1	175,000	118,000	360	27	17.0	
Clavacin	0.5	650	< 0.01	640	227	1.6	
Clavacin	0.1	65,900	54,500	5,000	6,900	343.0	
Fumigacin	5.0	7,300	7,500	62	262	1.1	
Fumigacin	1.0	80,200	65,000	1,720	270	2.8	
Chaetomin	5.0	< 0.1	< 0.01	< 0.01	< 0.01	9.4 ^d	
Chaetomin	1.0	126,000	188,000	18	185	40.0 ^d	

^a Numbers of bacterial cells, in thousands, at start—67,000.

^b Numbers of bacterial cells, in thousands, at start—10,000.

^c Numbers of bacterial cells, in thousands, at start— 450.

^d After 20 hours, control being, in thousands, 198.

stance, namely a dilution of only 1:20,000, was required to bring about complete sterilization of the culture. Fumigacin and chaetomin, substances that are largely active against gram-positive bacteria and exert only a limited bacteriostatic effect on gram-negative organisms of the *E. coli* type, stand midway between the other preparations. In lower concentrations, namely in 1:20,000 dilution, these two substances had little bactericidal action against *E. coli*; in high concentrations, 1:2,000, chaetomin was highly bactericidal and fumigacin also showed some activity.

A totally different relationship was obtained for the bactericidal action of the antibiotic substances against gram-positive bacteria, as represented by *S. aureus*. Actinomycin and penicillin proved to be highly effective bactericidal agents against this organism, the first bringing about a more com-

plete destruction of the bacterial cells. Streptothricin was the only substance that showed somewhat lower bactericidal activity against *S. aureus* as compared with *E. coli*; this is similar to the bacteriostatic properties of this substance. The other three substances exerted about the same type of bactericidal effect upon this gram-positive organism as they did upon the gram-negative *E. coli*, although to a somewhat greater extent.

The bactericidal action of the antibiotic substances against the plant pathogen *P. tumefaciens* was very similar to that against *S. aureus*. The former is somewhat more resistant to chaetomin than the latter. In this respect as well, the bactericidal action of the antibiotic substances is nearly comparable to its bacteriostatic action.

SUMMARY

A comparative study was made of the bacteriostatic and bactericidal effects of several antibiotic substances upon different plant-pathogenic bacteria, two animal pathogens, and two saprophytes, including both gram-positive and gram-negative forms. The antibiotic substances were isolated from antagonistic fungi and actinomycetes and varied greatly in the degree of their isolation and purification.

Plant-pathogenic bacteria were found not to vary greatly in their sensitivity to antibiotic substances from other bacteria. Greater differences were observed among different species than among the various sources from which the bacteria were isolated or their functions under natural conditions.

Some substances, notably actinomycin and penicillin, act largely against gram-positive bacteria and only to a limited extent against gram-negative organisms. In the case of actinomycin the sensitivity of the bacteria ranges from the spore-forming aerobic bacteria and cocci on the sensitive side of the spectrum to the *Escherichia*, *Aerobacter*, and *Serratia* on the resistant side. Penicillin, however, does not show exactly the same gradation in sensitivity, some gram-negative bacteria like *Neisseria* being sensitive and some gram-positive bacteria like *B. mycoides* being resistant.

Some substances, like streptothricin and clavacin, act alike upon gram-negative and gram-positive bacteria. These two substances also revealed certain marked differences, however, the first being much more selective in its action against the various bacteria than the second. Some gram-positive (*B. mycoides*) and gram-negative bacteria (*Ps. aeruginosa*) are very resistant to streptothricin and others are very sensitive (*B. subtilis*, *Brucella abortus*).

Two other antibiotic substances, fumigacin and chaetomin, showed intermediate activity upon the different bacteria between that of the other two groups of compounds. Although largely active against gram-positive bacteria and only to a very limited extent against the *E. coli* group, fumigacin and

chaetomin were also active against certain gram-negative organisms, especially some of the plant-pathogenic types.

The degree of sensitivity of bacteria to the various antibiotic substances can, therefore, be only very roughly based upon their staining reactions. The gram-stain is not the absolute determinant of the sensitivity of resistance of bacteria to different antibiotic substances. When more than one substance is tested, it is found that the different bacterial species show distinctly different antibiotic spectra. This points to greater physiological differences among the bacteria, as determined by their relative sensitivity to the antibiotic substances, than can be explained by mere differences in their staining characteristics.

No attempt is made to interpret the significance of the results presented here in terms of possible control of plant diseases caused by bacteria. The fact, however, that the microorganisms from which the antibiotic substances were isolated are normal soil inhabitants, makes these results highly suggestive.

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RELATIVE GROWTH OF FLOWER PARTS OF TWO SPECIES OF IRIS

HERBERT PARKES RILEY

It has been shown in a number of instances that the pattern of growth of a particular organ may be expressed in terms of the relative growth rates of the main dimensions of that organ. In an extensive comparison of twelve lines belonging to three or four species of cucurbits, Sinnott (1936) showed that the rate of relative growth of ovary length and width was different in each species and that the final shape of the fruit was determined by these rates plus duration of growth. In each case, the relative growth rate remained unchanged throughout the development of the fruit.

In *Iris fulva* and *I. heragona* var. *giganticaerulea* (Riley 1942) relative growth rates of the main radii of the developing ovary account for the shape of the ovary as seen in cross section and explain why fruits of the two species have different shapes during comparable developmental periods but almost the same shape when they are mature. In each species, the relative growth rate of two radii changes several times throughout development. Relative growth of the radii is due principally to relative growth of the ovary wall at those radii. Riley and Morrow (1942) and Riley (1943) found that in *Iris* ovaries the growth rate of any cellular region such as the ovary wall or the cellular region between two locules is determined by the rate and duration of cell division and the rate of increase in cell size following division but that during most of development cell multiplication is a much more important factor than cell expansion.

The ovaries of these two species are not only very much alike when the mature ovaries are viewed in cross section, but are also not very dissimilar in their general size and shape. The sepals and petals of *fulva*, however, are very different from those parts of *giganticaerulea*. It was the purpose of this study to determine to what extent relative growth rates control the pattern of development of the various flower structures. The plants of *giganticaerulea* are from a marsh alongside Bayou Barataria. Those of *fulva* are from an oak forest-cypress swamp transition at Thibodaux, from a similar region at Laplace, or from an oak forest growing along the side of the road between New Orleans and Bayou Barataria. All are from Louisiana.

Length and width of ovaries, sepals, petals, and floral tubes were measured from fresh material by means of dividers except for the smallest ovaries and tubes. These were fixed, embedded, and sectioned serially, and measurements were obtained from camera lucida drawings of median longitudinal sections. Ovary length was measured from the place where the ovary

is inserted on the flower stalk to the place where it joins the floral tube; measurements of width were obtained from the widest part of the ovary. Sepals and petals were measured from the place where the claw joins the floral tube to the tip of the blade; the width was always the widest part of the blade. It was considered desirable to study the relative growth in length of the claw and of the blade for the sepal and petal of each species. Measurements were plotted of the claws and blades of the sepals, but because the transition from the claw to the blade is more gradual in the petals, the attempt to analyze the relationship of the claw and blade of the petal was abandoned. For each study, measurements were plotted on double logarithmic paper; curves were then plotted by the method of least squares except for very short regions or for those in which the points showed exces-

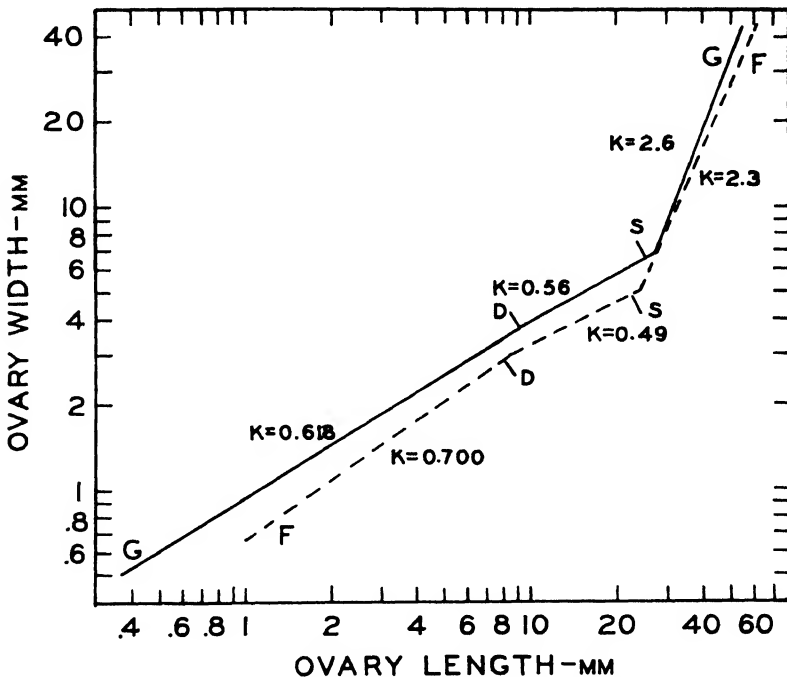


FIG. 1. Relative growth curves of ovary width and ovary length of *Iris fulva* (broken line) and of *Iris hexagona* var. *giganteaerulea* (unbroken line). D, completion of divisions of the nuclei of the embryo sac; S, fertilization.

sive scatter; these were plotted by inspection. The slopes, k , were calculated from Huxley's formula. The original measurements were in tenths of a millimeter and almost all measurements consisted of three significant figures. Four place tables of mantissas were used in converting the original measurements into logarithms. The values of k for the regions that were plotted by least squares were expressed to three significant figures. The slopes for the parts plotted by inspection were expressed in two significant figures.

OBSERVATIONS

Ovaries. When first organized, the ovary of *giganticaerulea* is wider in proportion to its length than is that of *fulva*. During early stages of growth, the ovary of *fulva* grows more rapidly in width relative to length than does that of the other species, but this relationship does not occur over a sufficiently long period for the two species to attain the same proportions (fig. 1). At about the time that the divisions of the nuclei in the embryo sac have been completed, the ovary of *giganticaerulea* is still proportionately wider than that of *fulva* but the difference is not so marked as in earlier stages. At that time the slopes change and the ovary of *giganticaerulea* increases proportionately somewhat more in width than does that of *fulva* until fertilization has been completed. After fertilization the *fulva* ovary is 24 mm. long while that of the other species is 28 mm. in length. When the ovary of *fulva* is 24 mm. long, it begins to grow much more rapidly in width than in length. This new relative growth rate is such that when this ovary is 28 mm. long, it has the same width as an ovary of *giganticaerulea* of the same length. For the remainder of development both ovaries increase much more rapidly in width than they do in length.

In both species the pattern of development is the same. The ovaries grow more rapidly in length than they do in width until after fertilization at which time both fruits increase more rapidly in width than in length. The reason for the first break in the curves is not clear, but the second is probably the result of the sudden and rapid growth of the seeds after fertilization.

Sepals. Differences in the shape and size of the mature sepals of the two species are much more marked than are differences in the ovaries (fig. 2). The mature sepal of *fulva* is mostly made up of the blade, for the claw occupies only about one-fifth of the length of the entire sepal. The blade is about twice as long as it is wide. The entire sepal of *giganticaerulea* is about 1.6 times as long as the sepal of *fulva* and the blade is 1.25 times as wide. The claw occupies about 40 per cent of the length of the sepal of *giganticaerulea*, and the blade is about 1.4 times as long as it is wide.

There is very little difference in the shape and size of the sepals of the two species when they are first formed, although that of *giganticaerulea* is slightly wider. The sepal of *giganticaerulea* increases in length relative to width somewhat more rapidly than does that of *fulva* until late in the development of the bud (figs. 3, 4). At that stage, the sepal of *fulva* is approximately 30 mm. long and the blade is slightly under 15 mm. wide while the sepal of *giganticaerulea* is 49 mm. long and the blade is 20 mm. wide. As the result of the somewhat more rapid growth in length in relation to width in *giganticaerulea* plus the attainment of a greater length, the sepal of *giganticaerulea* is about 2.5 times as long as it is wide, while that of *fulva* is only about 2.1 times as long when the first shift in the curves takes place.

When the sepals have attained this size, there is a very decided change in the slope of each curve and this is shortly followed by a second break in the curve. The slope of the second segment is difficult to interpret accurately as the segment is short and the points that determine the slope are few. This segment has been represented in figures 3 and 4 as a straight, horizontal line, which would indicate that the sepals were growing in length only and that they were not increasing in width during this period of relative growth. While this may not be strictly accurate, certainly the sepals are enlarging

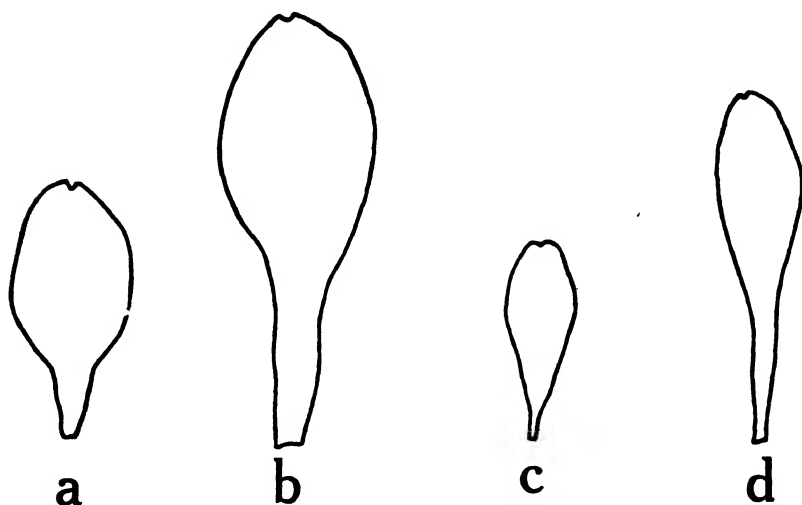
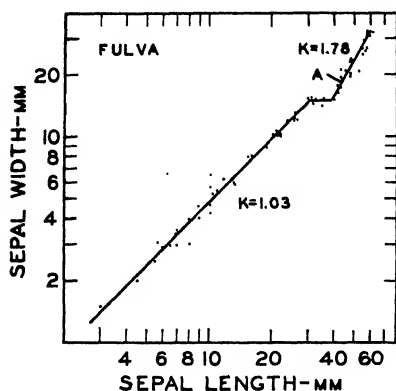


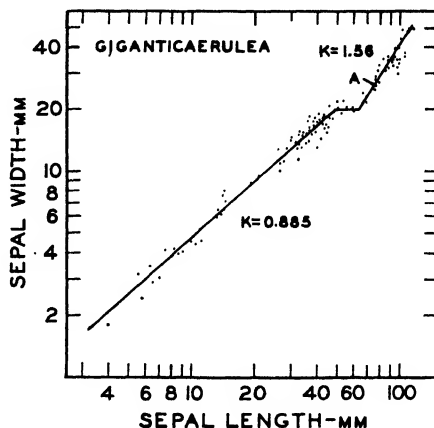
FIG. 2. Outlines of mature sepals and petals; a, sepal of *I. fulva*; b, sepal of *I. hexagona* var. *giganticaerulea*; c, petal of *I. fulva*; d, petal of var. *giganticaerulea*. Approximately $\times 0.4$.

much more rapidly in length than they are in width. To illustrate this more clearly, the actual points are plotted in figures 3 and 4, and the two curves are drawn separately. These double shifts in the curves appear to be real, characteristic features of the two curves and are neither seasonal variations nor clonal peculiarities. Relative growth of length and width of sepals from the same clones of *giganticaerulea* were studied during 1936, 1937, and 1938, and in each year this same feature of the relative growth curve was observed. Plants of *fulva* from Thibodaux were studied during 1937 and 1938; measurements were also obtained and plotted from clones growing in 1936 along the road to Bayou Barataria from New Orleans, and from a group of clones at Laplace in 1937. In all four instances the appearance of the curves was the same. If the interpretation of this double shift in the curves is correct, the sepals of both species increase in length only until that of *fulva* is 39 mm. long and that of *giganticaerulea* is about 65 mm. in length. The blades of the

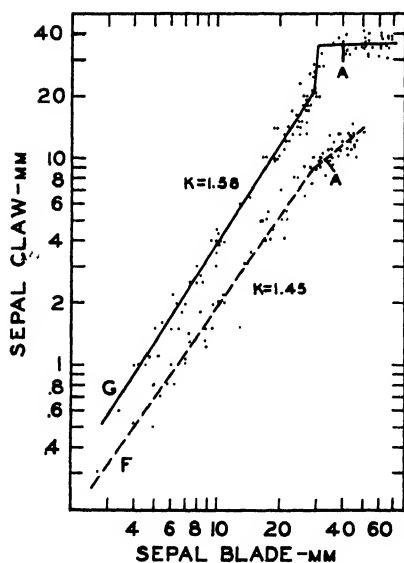
two species are still about 15 and 20 mm. wide respectively. When the sepals have reached these sizes, growth in width is again resumed. Until the flowers wither, the sepals of both species grow considerably more rapidly in width than in length.



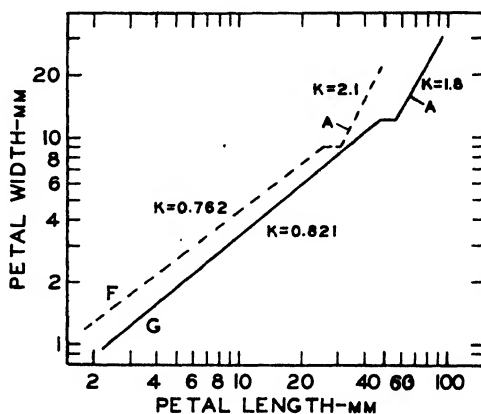
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5



6

FIGS. 3-6. Relative growth curves. FIG. 3. Sepal width and sepal length of *I. fulva*. FIG. 4. Sepal width and sepal length of *I. hexagona* var. *giganticaerulea*. FIG. 5. Length of claw of sepal and length of blade of sepal of both species. FIG. 6. Width of petal and length of petal of both species. A, anthesis.

The differences in the shape of the sepals of the two species at corresponding states of the development of the flower are due in part to differences in

the slopes of the lines in comparable parts of the curves but even more to the fact that the sepals of *giganticaerulea* become much larger than do those of *fulva*. For example, when the sepal of *fulva* is 30 mm. long, it is 2.04 times as long as it is wide, while a sepal of *giganticaerulea* of the same length is 2.33 times as long as it is wide. The difference in small part is due to an initial size difference but is due mostly to differences in relative growth rates. However, sepals of flowers in the same stages of development rather than sepals of the same length should be compared. A comparison of sepals 30 mm. long in the two species does not have much meaning for such a sepal is found in a flower of *fulva* in which the divisions of the embryo-sac nuclei have been completed but in a flower of *giganticaerulea* in which the four microspores have just been formed. When flowers of the two species are compared in which the embryo sac nuclei have completed their divisions, the picture is different. Such flowers of *giganticaerulea* are 49 mm. long and are approximately 2.5 times as long as they are wide. Therefore, not only differences in the relative growth rates but differences in the size of the structures at the same stage of development must be considered, provided that the relative growth rates do not change before this size is attained and provided also that the value of k in the two curves is not unity.

Since the sepal consists of two rather distinct parts, the claw and the blade, and since these two structures are proportionately very different in the two species, an analysis of the claw-blade relationship is of interest. Figure 5 shows that in *fulva* the claw grows more rapidly than does the blade until shortly before anthesis at the time when the second break occurs in the curves of sepal width against sepal length. The blade is initially almost ten times as long as the claw. Since this relative growth rate does not operate for a sufficiently long period, the claw never equals the blade in length, but at the time of the change in the slope of the curve, the blade is only about 3.2 times as long as the claw. During the remainder of development, the blade increases more rapidly than does the claw.

In *giganticaerulea*, the picture is very different (fig. 5). The sepal blade is initially about five times as long as the claw. The claw grows at a more rapid rate than does the blade, until the entire sepal is about 50 mm. long, at which time the blade is only about 1.25 times as long as the claw. There is then a very rapid increase in the length of the claw relative to that of the blade. The exact slope of this segment of the curve cannot be determined, but there is no doubt that the claw is growing relatively much more rapidly. When the sepal is about 65 mm. long, the blade is only about 0.86 times as long as the claw. The slope of the curve then shifts again, and the blade grows very much more rapidly than the claw. It is very difficult to determine the exact slope of the last two segments of this curve because the segments are short and the points are either too few or show too much scatter.

It is possible, however, that during the second segment of the curve there is practically no growth of the blade, while during the third segment, there is almost no growth of the claw.

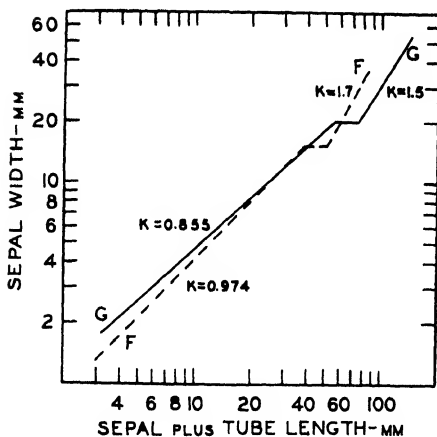
Undoubtedly, the difference in the claw is an important factor in determining the difference in the general shape of the sepals of the two species. When figures 3, 4, and 5 are studied together, the picture of sepal development is essentially the same in both species, except for relatively small differences in initial shape and in relative growth rates, until late in the development of the bud. From then until shortly before anthesis, the blade of *fulva* ceases to increase in width but both blade and claw continue to elongate and at the same relative rate as previously. In *giganticaerulea*, however, the blade ceases to grow both in width and in length, while the claw elongates considerably. The sepal of this species has a more spindly appearance in a late bud. During the opening of the flower, the sepal increases in width in both species; in *fulva*, both the blade and claw elongate, while in *giganticaerulea* the claw has ceased to grow in length.

Petals. Like the sepals, the mature petals differ considerably in shape in the two species, for that of *giganticaerulea* is about 1.75 times as long as that of *fulva* and very little wider (fig. 2). The claw of the petal of *giganticaerulea* is actually and proportionately much longer than the claw of the petal of *fulva*. When they are first organized, the petals of *fulva* are considerably wider than are those of the other species although the lengths are approximately the same. The petals of both species grow more rapidly in length than they do in width until late in the development of the bud (fig. 6). At this time the *fulva* petal is 25 mm. long and is 2.8 times as long as it is wide, while that of *giganticaerulea* is 47 mm. long and is 3.9 times as long as it is wide. At this stage of development of the flower, the petal of *giganticaerulea* is not only very much longer than that of *fulva* but is also considerably longer in proportion to its width.

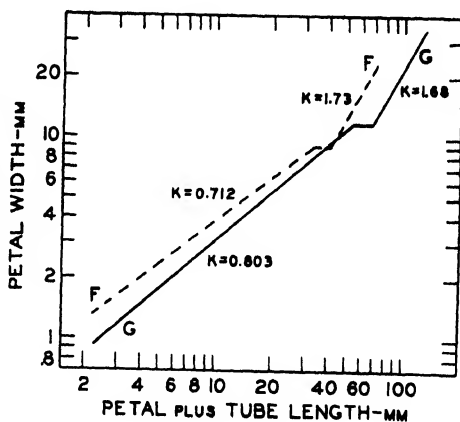
When the petals have reached this size, there is a double shift in the curves similar to the situation found in the curves of length and width of the sepals, and apparently the petals grow in length but not in width for a short period of the life cycle. During the last stages of the growth of the bud and during the expansion of the flower, the petals of both species grow much more rapidly in width than they do in length. The appearance of the curves of the same clones of *giganticaerulea* during three successive years is similar. The curves of *fulva* from Thibodaux during two different years and those from plants near Bayou Barataria in 1936 and from Laplace in 1937 were also similar. The general pattern of development of the petals is similar to that of the sepals, but there are considerable differences in the slopes and in the y-intercepts of the first and third segments of each species.

Sepal and Petal. When first measurable, the sepal of *fulva* is about 1.35 times as long as the petal of the same species. These two structures grow at almost the same rate ($k = 1.02$; $b = 0.72$) throughout development, so that when mature, the sepal is about 1.30 times as long as the petal. The relative sizes and relative growth rates are slightly different in the other species. When first organized, the sepal of *giganticaerulea* is 1.5 times as long as the petal. The petal elongates somewhat more rapidly than the sepal ($k = 1.07$; $b = 0.62$), and in the mature flower, the sepal is only about 1.2 times as long as the petal. In each species the relative growth rate is unchanged throughout development. The values of k are only slightly different in the two species and this slight difference might be due only to chance and therefore have no significance. However, for these two curves the points show remarkably little scatter and it is possible that the difference is real although not pronounced.

Floral Tube. In both species the floral tube increases much more rapidly in length than it does in width, measured at its greatest width. In *fulva* when



7



8

FIGS. 7, 8. Relative growth curves. FIG. 7. Width of sepal and combined lengths of sepal and floral tube. FIG. 8. Width of petal and combined lengths of petal and floral tube. Broken lines are curves of *I. fulva* and solid lines are curves of *I. hexagona* var. *giganticaerulea*.

tube width is plotted against tube length the slope of the line is 0.22 ($b = 1.62$) and in *giganticaerulea* it is 0.19 ($b = 2.11$). In each species there is no change in the relative growth rate during development. Since the floral tube is often considered to consist of part of the perianth and part of the stamens, the length of the floral tube was plotted against the length of the sepal above the floral tube and the greatest width of the sepal blade was plotted against the length of the sepal plus the length of the floral tube.

Tube length was also plotted against petal length, and the width of the blade of the petal was plotted against the combined lengths of petal and floral tube.

The tube elongates considerably more rapidly than does the sepal in each species. In *fulva*, $k = 1.62$ and $b = 0.028$, while in *giganticaerulea*, $k = 1.42$ and $b = 0.032$. The curves of sepal width against sepal length plus tube length (fig. 7) are generally similar to those of sepal width against sepal length alone, although the slopes and y-intercepts are somewhat different. It is to be expected that the curves might be similar, for the tube is relatively short when compared with the sepal. The relative growth curves of tube length against petal length are a single straight line for both species, but the slopes are considerably different. For *fulva*, $k = 1.60$ and $b = 0.048$, while for the other species, $k = 1.35$ and $b = 0.061$. The curves of petal width against petal length and tube length combined are in general similar to those of petal width against petal length although, as in the case of the sepals, the values of k and b are different (fig. 8).

Other Relationships. The sepals elongate more rapidly than do the ovaries. This is more pronounced in *giganticaerulea* ($k = 1.42$; $b = 1.02$) than in *fulva* ($k = 1.32$; $b = 1.55$). The petals also elongate more rapidly than do the ovaries. In *giganticaerulea*, $k = 1.49$ and $b = 0.70$, while in *fulva*, $k = 1.25$ and $b = 1.1$. In *giganticaerulea*, the petal grows slightly faster in relation to the ovary than does the sepal, but in *fulva* the petal and sepal elongate at almost the same rate relative to the ovary. This relationship is to be expected, since in *giganticaerulea* the petal grows somewhat faster than the sepal ($k = 1.07$) while in *fulva* they grow at approximately the same rate in relation to one another ($k = 1.02$).

The tube elongates considerably more rapidly than does either the sepal or petal in both species. Since the sepals and petals enlarge more rapidly than do the ovaries, the tubes should also grow in length more rapidly than the respective ovaries. When tube length is plotted against ovary length, $k = 1.93$ and $b = 0.035$ in *giganticaerulea*, while $k = 2.22$ and $b = 0.052$ in *fulva*.

Relative Growth Rate Ratios. An interesting relationship which may or may not have significance is found when the slopes of the various curves or segments of curves of *fulva* are divided by the slopes of the corresponding curves or segments of *giganticaerulea*. The quotients that are obtained for most of the curves and segments are listed in table 1. This table includes all the curves or segments of curves except those which would result in a ratio in the indeterminate form $0/0$, or the second and third segment of the curve of sepal claw against sepal blade where the slope of *giganticaerulea* is close to infinity or approximately zero. Nineteen quotients are listed for nineteen segments or curves which have been studied. They can be divided into four

groups. Ten curves or segments have a ratio between 1.13 and 1.19. It is possible, of course, that these actually represent six different ratios, but these ratios taken together show a deviation of only six in the third significant figure. This deviation does not seem too great to be due to chance and it seems reasonable to consider that these are all examples of one relative growth rate ratio between two species. One segment of one curve has a ratio of 1.03. This rate is found for the third segment of the curve of petal width against petal length plus tube length. The third segments of some of the curves are short and their points show some scatter, so it is possible that this segment and

TABLE 1. *Relative growth rates and relative growth rate ratios for nineteen curves or segments of curves.*

Ratio	Curve	Relative growth rates	
		<i>fulva</i>	<i>giganticaerulea</i>
1.19	Tube length and petal length	1.60	1.35
1.17	Petal width and petal length, segment III	2.1	1.8
1.16	Tube width and tube length	0.22	0.19
1.15	Tube length and ovary length	2.22	1.93
1.15	Sepal width and sepal length, segment I	1.03	0.885
1.14	Sepal width and sepal length, segment III	1.78	1.56
1.14	Sepal width and sepal plus tube, segment I	0.974	0.855
1.14	Tube length and sepal length	1.62	1.42
1.13	Sepal width and sepal plus tube, segment III	1.7	1.5
1.13	Ovary width and ovary length, segment I	0.700	0.618
1.03	Petal width and petal plus tube, segment III	1.73	1.68
0.95	Petal length and sepal length	1.02	1.07
0.93	Petal width and petal length, segment I	0.762	0.821
0.92	Sepal claw and sepal blade, segment I	1.45	1.58
0.89	Petal width and petal plus tube, segment I	0.712	0.803
0.89	Ovary width and ovary length, segment III	2.3	2.6
0.88	Ovary width and ovary length, segment II	0.49	0.56
0.87	Sepal length and ovary length	1.23	1.42
0.84	Petal length and ovary length	1.25	1.49

therefore its ratio are not so accurate as some of the other ratios. Three curves or segments have a ratio between 0.92 and 0.95 and may possibly be considered together. Five ratios vary from 0.84 to 0.89, and possibly represent one fundamental ratio.

If there were no relationship in relative growth between the two species the nineteen curves or segments could give nineteen different ratios and it is probable that at least a large per cent of the ratios would be different from one another. If the interpretation is admissible that the nineteen ratios can be grouped into four basic ones in which the variation is no greater than would be expected from random sampling and errors in measurements, a fundamental species relationship is indicated. It might be pointed out that in some cases it would be expected that the ratios would be the same because

of the nature of the curves. For example, the curves of sepal width against sepal plus tube should not be very different from the curves of sepal width against sepal length because tube length is proportionately very small when compared with sepal length. Such cases, however, are few. The fact that such different relative growth rates as tube width and length, sepal width and length, one segment of the curve of petal width and length, ovary width and length, tube length and petal length, and tube length and ovary length produce the same ratios would seem to indicate, at least, that there is a relationship between these species that expresses itself in the relative growth rates of various structures. The relative growth rate *ratios* of many curves or segments are the same even though the relative growth *rates* vary from 0.22 for tube width and length of *fulva* to 2.22 for tube length and ovary length of *fulva*. The fact that so many of the ratios are the same even though the rates themselves are very different supports the idea that a fairly simple relationship exists in the development of form in these two species.

SUMMARY

The ovaries of *Iris fulva* and *Iris hexagona* var. *giganticaerulea* grow more rapidly in length than in width until after the completion of the divisions of the nuclei in the embryo sac. From that time until after fertilization, growth in length is relatively even more rapid than previously. During fruit enlargement, the ovaries grow much more rapidly in width than in length. The rates are different in the two species for corresponding periods of development.

In *I. fulva*, sepal length, measured from sepal tip to the junction of the claw and floral tube, and sepal width grow at almost the same rate until fairly late in the bud; during this period the claw grows more rapidly in length than does the blade. During a short period before the opening of the flower, growth in width ceases and the sepal grows in length only; the relative growth rate of the claw and blade is the same as previously. During the opening of the flower, the sepal enlarges much more in width than in length and the blade grows more rapidly than the claw.

In var. *giganticaerulea*, the sepal grows more rapidly in length than in width and the claw grows much more rapidly than does the blade until a fairly late bud stage. The blade then ceases to grow in either dimension while the claw continues to elongate, so that, during this period, the sepal as a whole grows in length only. During the opening of the flower the claw does not grow, but the blade resumes growth and the sepal as a whole grows more rapidly in width than in length.

In each species the petals grow more rapidly in length than in width until the bud is almost fully grown. The petals then apparently increase in

length only until shortly before anthesis. During the last phase of development, the petals increase considerably more rapidly in width than in length.

In *I. fulva*, the petals and sepals elongate at almost the same rate but in var. *giganticaerulea* the petals increase in length a little more rapidly than do the sepals. The difference in the slope in the two species is very small.

The floral tube increases much more rapidly in length than in width in each species. The tube elongates more rapidly than does the sepal. The curve of sepal width against sepal length plus tube length is, in general, very similar to the curve of sepal width against sepal length alone in both species. Similarly, the curves of petal width against petal plus tube resemble those of petal width against petal length, although in the case of both sepal and petal the slopes and y-intercepts of the first and third segments are different.

In both species, the sepals, petals, and floral tubes elongate more rapidly than do the ovaries.

For nineteen curves or segments of curves, the slope of *I. fulva* was divided by the slope of var. *giganticaerulea* to produce a relative growth rate ratio. Allowing for errors of sampling and measurement, these nineteen curves or segments can be grouped into four basic ratios. Ten curves or segments have a ratio from 1.13 to 1.17; one has a ratio of 1.03; three have a ratio from 0.92 to 0.95; and five have a ratio of 0.83 to 0.89. Similar ratios are found even for different structure such as ovaries, sepals, and petals, and even though the relative growth rates, themselves, in many instances, are widely different. This constant repetition of a few ratios probably indicates a simple growth rate relationship between the two species.

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INFLUENCE OF LIGHT ON THE INFECTION OF WHEAT BY THE POWDERY MILDEW, *ERYSIPHE* *GRAMINIS TRITICI*

ROBERTSON PRATT

The work of Reed (1914), who concluded that the effect of light on the infectiousness of barley and wheat mildews was due to the influence of the light on the development of chlorophyll in the host plant, suggested a close connection between mildew infection and the carbohydrate supply in the host.

Trelease and Trelease (1929) verified this connection. They found that the powdery mildew, *Erysiphe graminis tritici*, easily infected wheat leaves in either light or darkness provided an adequate source of carbon was available, and they concluded that there is a direct correlation between mildew development and the amount of carbon available in the host. More recently Allen (1942) has furnished interesting quantitative evidence that in heavily infected leaves carbohydrate is the primary substrate that is oxidized, although toward the end of the infection other substrates are also oxidized. Trelease and Trelease (1929) also showed that inoculated plants in the light but deprived of carbon dioxide were incapable of supporting mildew, but that if these same plants were supplied with appropriate sugar solutions, the mildew developed despite the lack of carbon dioxide. The fungus evidenced no tendency to spread into the solution but remained strictly limited to the host. Yarwood (1934a) noted a similar phenomenon and observed that within limits the susceptibility of clover leaflets to species of *Erysiphe* increased as the concentration of the sugar solution on which the leaflets were floated increased. The primary purpose of the present investigation was to study quantitatively the effect of different daily periods of illumination on the infection of wheat, *Triticum vulgare*, by the powdery mildew, *Erysiphe graminis tritici*.

The comparative freedom of plants from mildew infestation in sunny seasons or locations has been attributed not only to the relatively high temperatures then or there prevailing but, in part at least, to ultra-violet radiation in sunlight. Hey and Carter (1931), using a quartz mercury vapor lamp as a source of ultra-violet radiation, were sometimes able to check partially an attack of mildew without appreciably injuring the host plant. In the present study, the influence of different spectral regions upon spore germination was also investigated.

METHODS

The methods employed were the same as those previously described (Pratt 1943). Hanging-drop cultures were used for studies involving the fungus alone, and for studies involving mildew cultures on the host plants a thermostatic chamber (Trelease 1925) so arranged that it could be illuminated from above was employed. The techniques of inoculation and of culturing stock plants were the same as those used previously (Pratt 1943).

RESULTS

Development of Mildew on Living Plants under Different Daily Periods of Illumination. To ascertain the minimum daily exposure to light that would permit mildew development on wheat plants under the experimental conditions, plants that had been in darkness for 24 hours to free them of surplus carbohydrates immediately before treatment were inoculated in the usual manner and then were subjected to different periods of illumination. The source of light was a 1000-watt clear Mazda-C electric light lamp provided with a reflector that was suspended approximately four feet above the plants. The data that were obtained are shown in table 1.

TABLE 1. *Effect of day length upon incubation period and maturation period of powdery mildew on Marquis wheat.*

(1) Temp.	(2) Daily illumination, hours	(3) Av. incubation period, ^a days	(4) Av. time for appearance of conidia, days	(5) Av. maturation period, ^b days	(6) Matura- tion Period Incuba- tion Period	(7) Viru- lence of infection (approximate)
10° C	1	7.75	12.50	4.75	0.613	+
	3	7.25	11.50	4.25	0.587	++++
	6	6.75	10.25	3.50	0.519	++++
	12	6.50	10.00	3.50	0.538	++++
	24	6.25	9.25	3.00	0.480	++++
20° C	1	3.25	5.00	1.75	0.539	+
	3	2.75	4.00	1.25	0.455	++
	6	2.50	3.50	1.00	0.400	++++
	12	2.25	3.00	0.75	0.333	++++
	24	2.50	3.50	1.00	0.400	++++
25° C	1	3.75	6.00	2.25	0.600	+
	3	3.25	4.50	1.25	0.384	++
	6	2.50	3.50	1.00	0.400	++++
	12	2.50	3.75	1.25	0.500	++++
	24	2.50	3.75	1.25	0.500	++++

^a Time elapsed between inoculation of the plants and the first macroscopic signs of infection.

^b Time required for appearance of first conidia minus incubation period.

No readily distinguishable differences in the virulence of the infection that finally occurred were observed until the period of illumination was reduced to three hours daily at 20° and 25° C, or to one hour daily at 10° C, although a notable delay in the time required for development was noted at 10° C when the plants were illuminated less than six hours in each twenty-four. It is probable that under the experimental conditions used about one hour is the minimum daily exposure to light which will permit elaboration by the host of sufficient requisite materials to maintain it in a condition suitable for support of mildew. Abundant development of the mildew did not occur at any temperature when plants were illuminated less than three hours daily. The decreasing trends, of the values given in column 6, indicate a tendency for the length of the maturation period with respect to the incubation period (both periods being determined purely arbitrarily) to decrease with increasing daily periods of illumination, at least for cultures at 10° C and 20° C. The data for cultures at 25° C are somewhat erratic, but they may indicate a similar trend.

The virulence of infection with a three hour daily period of illumination was greater at 10° C than at 20° C or 25° C (column 7). Possibly this is correlated with the relative rates of respiration and of photosynthesis in the host. Development of the parasite undoubtedly depends upon the ability of the host tissues to furnish a continuous supply of suitable nutrient substrates. In view of the obligate parasitic habit and the high degree of physiological specialization of the fungus, it is reasonable to assume that some of its essential metabolites are compounds that are in no way by-products, but are essential reactants in some step of the metabolism of the host. One can, therefore, think of the host and the parasite as competing for some essential substrate. At the higher temperature, destruction of this substrate or some important intermediate in the host might very conceivably proceed more rapidly than its synthesis. Thus a deficiency of the requisite compounds might occur. Possible support for this suggestion is offered by the generally somewhat higher Q_{10} values for respiration than for photosynthesis (Miller 1938; Spoehr 1926). The increased respiratory rate in host tissues that are infected with powdery mildews may also be of considerable importance in this connection. Yarwood (1934b) reported an increase of 41 per cent in the respiration of clover leaflets infected with mildew, and Pratt (1938), Allen and Goddard (1938), and Allen (1942) found increases of from 250 to 650 per cent in the respiration of wheat infected with *Erysiphe graminis tritici*. Such studies have not been made at a series of temperatures, but one might expect less acceleration of the respiration at the lower temperature, and a consequent conservation of the respiratory substrate which is presumably essential also for the growth of the mildew. Allen's observations (1942) on damage to the photosynthetic mechanism and on changes in soluble sugar content in infected plants also are in accord with the suggestion made above.

Comparative Development of Mildew on Living Plants in Light and in Darkness. It seemed desirable to determine how far development of the mildew might proceed on the living host in darkness. Accordingly, ten pots of wheat plants previously in darkness 24 hours were inoculated. They were then divided into five pairs and one pot of each pair was kept in darkness and one was exposed to twelve hours of illumination daily, at each of five different temperatures. At regular intervals leaves were fixed and bleached in alcohol, cleared in a saturated solution of chloral hydrate, and subsequently mounted in lacto-phenol-aniline blue for microscopical examination. The cycle of powdery mildew development from conidium germination to conidium formation was arbitrarily divided into ten stages that could be easily and unmistakably recognized under the microscope. From table 2 it is easy to determine the stage of development attained in either

TABLE 2. *Effect of temperature upon rate of development of powdery mildew on Marquis wheat in light and in darkness*

Figures are times in hours

Stage of development	10° C		15° C		20° C		25° C		30° C	
	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light
1. Germination of conidia	12 (few) 24 (many) 48 (many)	12 (few) 24 (many) 48 (many)	12	12	12	12	12	12	Very sparse after 12 hrs. Spores appear coagulated	
2. Penetration of host epidermis	24-48	24-48	24	24	24	24	24	24		
3. Haustorium initial formed	72	72	24 (?) 48	24 (?) 48	24	24	24	24
4. Haustorium fingers formed	96 (?)	72-96	48 (?)	48	48	48	48	48
5. Superficial mycelium sparse	(?)	96 very sparse	72-96 (very few patches)	72	48	48	48	48
6. Haustorium fingers elongated	120-144	120	72-96 (very few)	72	72	72	72	72
7. Superficial mycelium moderately abundant	144	96	96	72	72
8. Superficial mycelium abundant	192	120	96	96
9. Conidiphores forming	216	120	120	72-96 (?)	120	96 (???)
10. Conidia present	216	120	72-96	96

light or darkness in a given time under the experimental conditions used. The data in table 2 refer to stages of development as seen microscopically and no reference is made here to the relative virulence of the mildew infection at different temperatures. Although in no case was the fungus able to complete its cycle by producing conidia when kept continuously in the dark, it should be noted that for the first two to three days after inoculation development of the mildew proceeded at approximately the same rate in both the light and the dark. Sufficient carbohydrate reserves probably were available in the host to satisfy the requirements of the mold during this period but became depleted in the absence of light before development could be completed. Although conidia were never formed in darkness, conidiophores began to form from the rather meager vegetative mycelium on a few plants at 20° C and 25° C. At those temperatures the rate of development was the same in light and darkness up to the stage at which the superficial mycelium commences to spread. At that point development of the fungus in darkness was checked, however. At lower temperatures—i.e., 10° C and 15° C—development was arrested at an earlier stage. At 30° C germination was poor and no further development occurred. Spores that had been on leaves at 30° C for twelve hours had the same granular and coagulated appearance mentioned previously (Pratt 1943) as characteristic of spores in hanging drops at 35° C. It should be emphasized that the figures in table 2 are merely approximations and represent the time at which the particular stage described appeared to be the most common one to be seen.

TABLE 3. *Effect of quality of radiant energy upon germination of spores of Erysiphe graminis tritici in tap water at 20° C.*

Region of spectrum	Radiant energy (ergs/mm. ² /sec.)	Percentage germination
Ultra-violet	6.04	49.7
Blue	6.20	76.1
Green-yellow	6.37	54.5
Short red	6.37	55.1
Long red	6.37	52.6
White light (From Mazda lamp)	8.8	54.8
Control in darkness	71.9

Effect of Light on Germination of Spores. Table 3 shows the results obtained when different sets of mildew spores were germinated on tap water at 20° C for eight hours in darkness and in different regions of the spectrum. All viable spores germinated within eight hours under the conditions of these experiments (see solid curve in figure 1). The relative distribution of the energy values from the different light sources is shown in figure 2, the legend of which also indicates the source of light for each of the wave lengths employed. In each germination test at least 1500 spores

were counted, a sufficiently large number to yield reliable results. All but one of the wave lengths of light that were studied partially suppressed spore germination. Truly critical evaluation and interpretation of the data

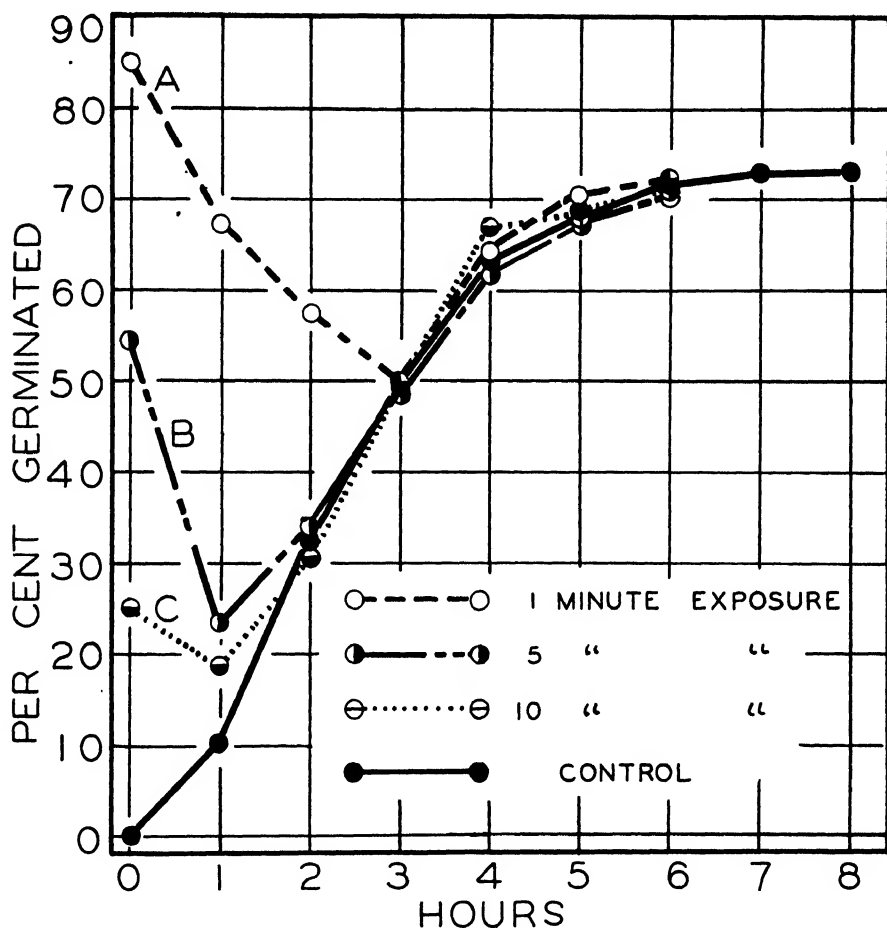


FIG. 1. The solid curve represents the percentage germination of normal *Erysiphe* spores at hourly intervals. Curves A, B, and C represent the percentage of the spores that were germinated after twenty-four hours when the cultures were irradiated for one, five, and ten minutes, respectively, with ultra-violet radiation (principally 365μ) after immersion in water for the number of hours indicated on the abscissa. (See text for further explanation.)

in table 3 are impossible without more knowledge than is now available of the mildew spores and the compounds of which they are composed. It may be suggested tentatively, however, since no significant effect was noted in the blue light (436μ), that one or more compounds present in the spores has its minimum absorption (which may be zero) at that wave length and

that the absorption increases as the wave length deviates each way from 436 μ . Further speculation at this time is not warranted by the data, but

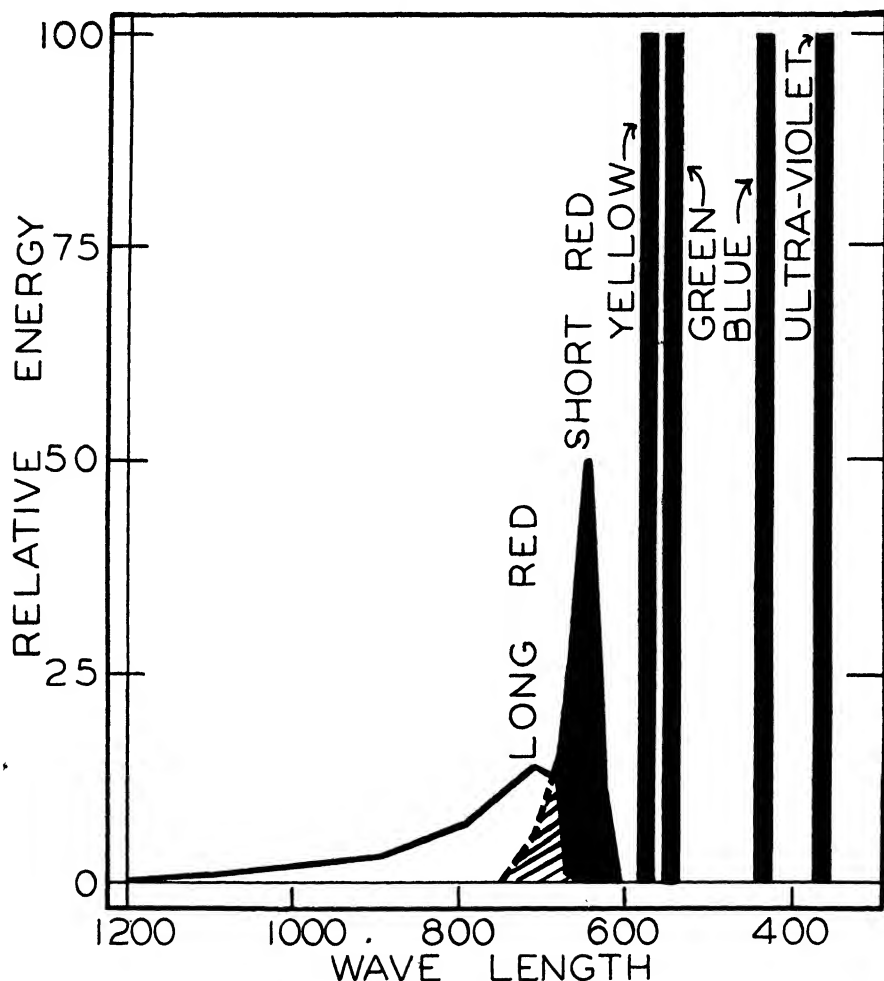


FIG. 2. Distribution of the energy emitted by the different filter combinations and light sources in selected regions of the spectrum. The different points on each curve were obtained by multiplying together the filter transmissions and the radiation values of the sources at the given wave lengths and adjusting the areas under the curves to equivalent values. The source and filter combinations used were as follows: *long-red*—1000 watt lamp, Schott glass filters No. RG 5 (2 mm.) + VG 3 (1 mm.) + H₂O, 5 cm.; *short-red*—1000 watt lamp, Corning filter No. 243 + copper sulphate, 1.2 per cent solution 5 cm. deep + H₂O, 5 cm.; *yellow-green*—quartz mercury arc, tartrazine in gelatine filter + quinine hydrochloride, 0.4 per cent solution 5 cm. deep + copper sulphate, 10 per cent solution 2 cm. deep (this combination gave about equal transmission of the yellow and green lines); *blue*—quartz mercury arc, crystal violet in cellophane filter + quinine hydrochloride, 0.4 per cent solution 5 cm. deep + copper sulphate, 20 per cent solution 2.5 cm. deep; *ultra-violet*—quartz mercury arc, Corning filter No. 586 + copper sulphate, 3 per cent 1 cm. deep. Wave lengths are in millimicrons.

it may be noted in passing that several biological compounds, including some enzymes, are known to possess such characteristics (Miller 1939).

Figure 1 actually represents two graphs, one superimposed upon the other. It shows the percentage germination of *Erysiphe* spores on tap water at successive hourly intervals and also the sensitivity of *Erysiphe* spores to ultra-violet radiation (365μ). The solid curve is a control and first should be considered alone and entirely apart from the other curves in the figure. It represents the percentage germination of the mildew conidia at hourly intervals on hanging drops of tap water. Since maximum germination (approximately 75 per cent) of the spores occurred in eight hours, the curve was not extended beyond that point although the observations were carried out for 24 hours.

Now the other curves may be considered in conjunction with the solid curve. Different groups of spores on tap water were exposed to the unshielded radiation from a four-inch quartz mercury arc at a distance of 32 cm. for periods of one, five, and ten minutes, after different periods of soaking in water. Thus one set consisting of three groups was irradiated at zero time; another set of three groups was irradiated after one hour of soaking, another after two hours, *et cetera*. Spores were in darkness the entire time they were not being irradiated. Germination counts of all experimental cultures were made 24 hours after irradiation and are represented by the points plotted in curves A, B, and C. The ordinates for the points plotted in curves A, B, and C indicate the percentage germination 24 hours after irradiation of the drops and the abscissas represent the length of time the spores were immersed in water before they were irradiated. Since the solid curve represents the percentage germination of normal spores at the times indicated on the abscissa, it also indicates the percentage of spores in the experimental cultures that had already germinated at the times the different sets of drops were irradiated. Thus at each point the vertical distance between a curve for any irradiated culture (broken line A, B, or C) and that for the control culture (solid curve) represents the percentage of spores in that experimental set which germinated after irradiation. Although only 74.8 per cent of the control spores germinated in 24 hours, 85.3 per cent of those irradiated for one minute at the time of mounting the preparation (zero time) germinated in the same length of time. Maneval (1927) found that the teliospores of each of thirty species of rusts required definite rest periods for physiological maturation before germination could occur and it seems possible that the ultra-violet radiation in these experiments caused an artificial maturation of some sort, as has been described for the fruits of some higher plants, thus rendering about 10 per cent more of the conidia viable. Longer exposures to the radiation were injurious from the start. After the spores had become more hydrated, even the short exposure was

detrimental to them. The injury increased as more water was taken up, so that after three hours of soaking all viable but ungerminated spores were killed by exposure for one minute to radiation from this source. All viable but ungerminated spores were killed by exposure for five minutes or more after two hours of soaking. The suggestion may be offered that increased sensitivity after hydration of the spores was due to an alteration of the molecular configuration of their constituents and that this alteration tended to increase the absorption at the $365\ \mu$ wave length. Similar phenomena were not observed at the other wave lengths that were studied.

It is considered that the principal new contributions of the present work are the microscopical observations on the rate and comparative degrees of development of the powdery mildew infection on wheat leaves in the light and in the dark and the observations on the influence of ultra-violet and other radiation on the mildew spores.

SUMMARY

A study was made of the effect of the length of daily period of illumination upon the infection of wheat (*Triticum vulgare*) by the powdery mildew, *Erysiphe graminis tritici*. The influence of irradiation from several different regions of the spectrum upon germination of *Erysiphe* spores was also observed.

Infection of wheat occurred when the plants were illuminated for as little as one hour each day, although the virulence of the infection was somewhat reduced. A three-hour daily period of illumination, however, permitted development of heavy infection. In total darkness, the spores of the parasite germinated and the young mycelia penetrated the host tissue, but the fungus died before sufficient growth occurred for it to become visible macroscopically.

It was found that the blue light (wave length $436\ \mu$) with intensity of $6.2\ \text{ergs/mm.}^2/\text{sec.}$ exerted no effect upon the germination of *Erysiphe* spores. All other regions of the spectrum that were studied at a similar energy value seemed to cause an appreciable reduction in the percentage of spores that germinated in tap water. The spores were highly sensitive to the ultra-violet radiation from a quartz mercury arc and their sensitivity increased as they became more hydrated.

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THE RANDOMNESS OF CHROMOSOME DISTRIBUTION
AT ANAPHASE I IN AUTOTRIPLOID
LOLIUM PERENNE L.¹

W. M. MYERS²

It has been assumed generally that the third set of chromosomes of triploids is distributed at random during meiosis except for the loss due to lagging. Consequently, it is expected that gametes will be produced with chromosome numbers ranging from haploid to diploid in an approximately binomial frequency (Darlington 1937). This hypothesis has been tested with adequate data in only one species. Satina and Blakeslee (1937a) determined the chromosome assortment in the first division of meiosis in 1,000 pollen mother cells of triploid *Datura stramonium*. When compared with the frequencies expected on the basis of binomial distribution of extra chromosomes from the trivalents, they found an excess of the assortments from 12-24 to 15-21, inclusive, and a deficiency of the 17-19 and 18-18 assortments. Furthermore, the deviations of observed from expected were so great as to leave no question of their statistical significance. In a smaller sample of macrospore mother cells of triploid *Datura*, these authors (1937b) found a similar deviation of observed assortments from expected. On the basis of their results, Satina and Blakeslee (1937a) concluded, "Despite the lack of direct evidence from other forms than *Datura*, it seems probable that the divergence of the assortments at the I division in P.M.C. from calculated values is of general occurrence and is to be attributed to the nature of chromosomes and the mechanisms involved in their movements at division."

The concept of random assortment of the extra chromosomes in triploids and the discrepancies found by Satina and Blakeslee (1937a, b) are of such importance in an understanding of chromosomal behavior during meiosis that it seems imperative that the hypothesis be tested in triploids of other forms. Meiotic behavior of an autotriploid plant of *Lolium perenne* L. was reported by Myers (1943), but at that time too few data were available from anaphase I to provide a critical test of the hypothesis. The triploid plant studied previously was lost, but two more were obtained from crosses of autotetraploid with diploid plants. The present investigation deals with the occurrence and position of univalents at metaphase I and the chromosome numbers in the daughter groups at anaphase I in these two plants.

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MATERIALS AND METHODS

The two triploid plants were grown in pots in the greenhouse during the winter of 1942-1943. Flowering was induced by use of supplementary illumination to provide a 16-hour daily light period. The microsporocyte material was fixed in acetic alcohol and was examined as soon as possible, all determinations being made within a few days following fixation. All data were taken and the photomicrographs were made from fresh aceto-carmin smear slides. Material was collected from one plant on four different dates. Metaphase I data were taken from only one collection, but anaphase I distributions were counted in all four. Since the chromosomes were not well spread at anaphase I in the second plant and accurate counts were obtained with difficulty, only one collection was made from this plant.

Data were recorded only for anaphase I sporocytes in which both chromosome groups could be counted with certainty. In this manner, the greater ease of counting groups with low numbers was balanced by the correspondingly greater difficulty of counting those with higher numbers.

EXPERIMENTAL RESULTS

Univalents at Metaphase I. Univalent chromosomes at metaphase I are more common in triploid *Lolium perenne* (Myers 1943) than in triploid

TABLE 1. Number and percentage of metaphase I sporocytes with various numbers and positions of oriented and unoriented univalents

Frequency of metaphase I sporocytes showing indicated arrangement of unoriented univalents											
	0	0-1	1-1	0-2	1-2	0-3	2-2	1-3	0-4	Sub total	
No oriented univalents											
No.	402	587	226	266	125	61	15	28	10	1720	
Per cent	16.1	23.5	9.1	10.7	5.0	2.4	0.6	1.1	0.4	69.0	
One oriented univalent											
No.	200	191	60	62	27	7				547	
Per cent	8.0	7.7	2.4	2.5	1.1	0.3				21.9	
Two oriented univalents											
No.	96	51	14	14						175	
Per cent	3.8	2.0	0.6	0.6						7.0	
Three oriented univalents											
No.	15	7								22	
Per cent	0.6	0.3								0.9	
Four oriented univalents											
No.	4									4	
Per cent	0.2									0.2	
Grand Total										2494*	
										100.0	

* Includes 26 sporocytes (1.0 per cent) with five univalents.

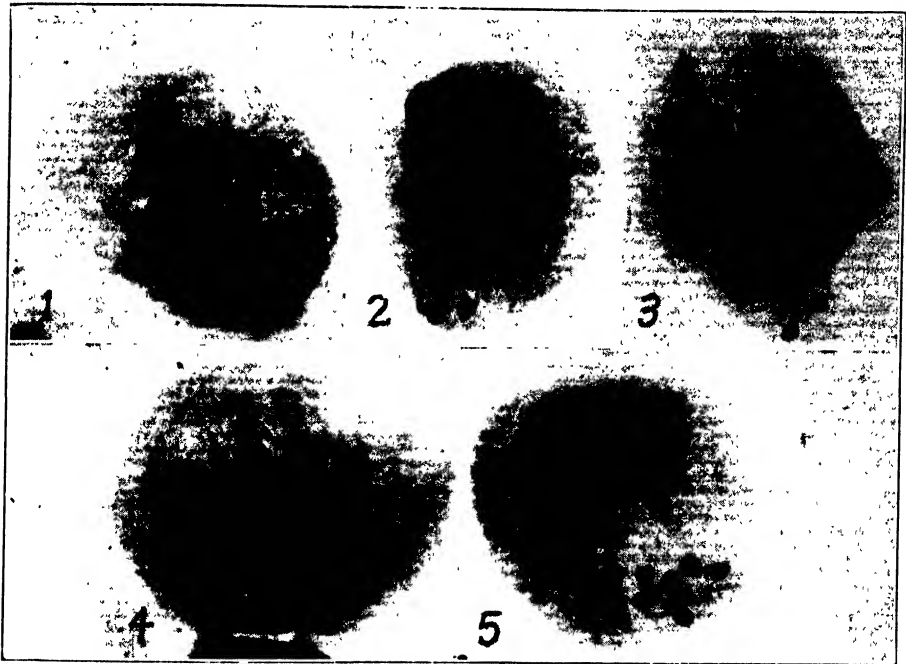
Datura stramonium (Satina and Blakeslee 1937a). Since, as will be shown later, the position of the metaphase I univalents may influence the distribution at anaphase I, this factor is of considerable importance. A total of 2,494 metaphase I sporocytes was recorded (table 1). Sixteen per cent had only trivalents; the remainder had one or more univalents, with a maximum of five observed in 1 per cent of the cells. In 69 per cent of the cells (including the 16 per cent without univalents), there were no univalents oriented on the equatorial plate with the bivalents and trivalents, while there was one oriented univalent (fig. 1) in 22 per cent of the cells, two in 7 per cent, three in 0.9 per cent, and four in 0.2 per cent.

Univalents oriented in this manner at metaphase I would almost certainly lag and divide equationally at anaphase I. Such oriented univalents do not account, however, for all of the anaphase I laggards. There were 69 per cent of the metaphase I sporocytes without oriented univalents, but only 43 per cent of 1,636 anaphase I cells without lagging and equationally dividing chromosomes. Similar comparisons for one, two, three, and four oriented univalents at metaphase I and laggards at anaphase I, respectively, were 22 per cent and 31 per cent; 7 per cent and 18 per cent; 0.9 per cent and 7 per cent; 0.2 per cent and 1.4 per cent. No doubt some of the univalents which were near the equatorial plate but recorded as not oriented would have been oriented at a slightly later stage of metaphase I or at early anaphase I. Also, some of the excess of laggards probably arose from the disjunction of trivalents in the manner described by Darlington (1929, 1937) and Myers (1943).

The univalents that were not oriented on the equatorial plate were found in positions ranging from near the main group of chromosomes to near the poles. Where two such univalents occurred in the sporocytes having no oriented univalents they were found to lie on the same side of the equatorial plate (0-2 position) in 266 sporocytes (fig. 2), and one on each side (1-1 position) in 226 sporocytes. The fit of the observed ratio to the expected 1:1 was satisfactory as shown by X^2 ($0.10 > P > 0.05$). It is apparent (table 1) that the 1-1 and 0-2 positions likewise occurred in approximately equal frequencies in the sporocytes with one and with two oriented univalents. With three unoriented univalents the 1-2 and 0-3 (fig. 3) positions are expected in a 3:1 ratio. Among the sporocytes without oriented univalents, the distribution of these two types deviated significantly from expected (X^2 gave $0.02 > P > 0.01$). On the other hand, the fit to a 3:1 ratio was good for the sporocytes with a single laggard. In cells with four unoriented chromosomes, positions 2-2, 1-3, and 0-4 (fig. 4) are expected in a 3:4:1 ratio and the fit of observed to calculated was satisfactory when tested by X^2 ($0.30 > P > 0.20$).

The results indicate that in general the unoriented metaphase I univalents occur on either side of the equatorial plate at random.

Influence of Metaphase I Univalents upon Distributions Expected at Anaphase I. The influence of the position of unoriented metaphase I univalents upon expected frequencies of various anaphase I distributions is shown in table 2. At anaphase I in this material, no group was observed with less than seven chromosomes. It is probable that one chromosome from each bivalent and trivalent almost invariably moves to each pole at anaphase I. The third chromosome of the trivalents might be expected to pass to either



Metaphase I and anaphase I of meiosis in triploid *Lolium perenne*. Ca 840 \times . FIG. 1. Metaphase I with one oriented univalent. FIG. 2. Two unoriented univalents in 0-2 position at metaphase I. FIG. 3. Three unoriented univalents in 0-3 position at metaphase I. FIG. 4. Four unoriented univalents in 0-4 position at metaphase I. FIG. 5. Anaphase I with one lagging and dividing univalent and a 9-11 chromosome distribution.

pole strictly at random, in which case the distribution of the extra seven chromosomes may be calculated from $(\frac{1}{2} + \frac{1}{2})^7$ (table 2). In sporocytes with one unoriented univalent the distribution likewise should fit the binomial $(\frac{1}{2} + \frac{1}{2})^7$ if it is assumed that the position of the univalent is independent of the distribution of extra chromosomes from the trivalents. When there are two univalents, both unoriented, the expected distribution differs appreciably from the binomial $(\frac{1}{2} + \frac{1}{2})^7$, whether the position of the univalents is 1-1 or 0-2 (table 2). If, on the other hand, these two positions occur with equal frequency, the average of their anaphase I assortments will be exactly like that expected from the random distribution of seven chromo-

somes. A similar situation obtains for three unoriented univalents, the expected average anaphase I assortments fitting the binomial $(\frac{1}{2} + \frac{1}{2})^3$ if the 1-2 and 0-3 positions of the univalents occur in a 3:1 ratio. The same average of anaphase I distributions is expected from sporocytes with four unoriented univalents if the 2-2, 1-3, and 0-4 positions occur in a 3:4:1 ratio.

There may be calculated also the expected ratios of anaphase I distributions when there are one, two, and three lagging chromosomes (oriented metaphase I univalents). In these cases, too, the unoriented metaphase I univalents will not affect the ratio of anaphase I assortments if their positions relative to the equatorial plate are at random.

TABLE 2. *Frequencies of different anaphase I distributions, calculated on the assumption of random disjunction of third chromosome of trivalents, expected from metaphase I sporocytes with no oriented and various numbers of unoriented univalents.*

Number and position of univalents at metaphase I	Percentage of sporocytes with indicated distribution of anaphase I			
	7-14	8-13	9-12	10-11
0	1.56	10.94	32.81	54.69
0-1 ^a	1.56	10.94	32.81	54.69
1-1	0	6.25	31.25	62.50
0-2	3.12	15.62	34.38	46.88
1-2	0	6.25	31.25	62.50
0-3	6.25	25.00	37.50	31.25
2-2	0	0	25.00	75.00
1-3	0	12.50	37.50	50.00
0-4	12.50	37.50	37.50	12.50

^a The position of the univalents relative to the equatorial plate. 0-1 indicates a single univalent, 1-1 indicates two univalents, one on each side of the plate, 0-2 indicates two univalents on one side, etc.

The calculations for table 2 and comparisons with univalent positions shown in table 1 are based on the premise that oriented metaphase I univalents lagged at anaphase I while unoriented univalents were included in the daughter chromosome group at the pole near which they lay. It was shown from comparisons of frequencies of oriented univalents and anaphase I laggards that some of the unoriented univalents probably later became oriented and lagged at anaphase I. This might be expected to occur at random so that the relative frequencies of complementary types, i.e., 1-1 with 0-2 positions, etc., will remain unchanged. Since the data presented in table 1 indicated a general tendency for the unoriented univalents to lie on either side of the equatorial plate at random (relative to other univalents), it appears legitimate to calculate the frequencies of different anaphase I assortments by the expansion of $(\frac{1}{2} + \frac{1}{2})^7$ for sporocytes without laggards, $(\frac{1}{2} + \frac{1}{2})^6$ for sporocytes with one laggard, $(\frac{1}{2} + \frac{1}{2})^5$ for sporocytes with two laggards, and $(\frac{1}{2} + \frac{1}{2})^4$ for sporocytes with three laggards.

Chromosome Assortment at Anaphase I. In the four collections from plant 2, counts of chromosome numbers were obtained from a total of 641 anaphase^{*} I sporocytes without laggards (table 3). The fit of the total observed ratio to expected on the basis of random assortment was satisfactory as indicated by the X^2 test ($0.20 > P > 0.10$). Values of $P > 0.05$ also were obtained for the data from collections 1 and 3 from this plant but with the data from collections 2 and 4, the deviations of observed from calculated

TABLE 3. *Observed and calculated numbers of four types of anaphase I distributions in sporocytes without lagging chromosomes.*

Source of data		Number of anaphase I with indicated distribution					X^2 for	
		7-14	8-13	9-12	10-11	Total	3 D/F	2 D/F ^a
Plant 2, Coll. 1	Obs.	1	15	41	102	159		
	Cal.	2.5	17.4	52.2	87.0	159	6.208	5.751
Coll. 2	Obs.	9	21	65	127	222		
	Cal.	3.5	24.3	72.8	121.4	222	10.358	1.284
Coll. 3	Obs.	2	23	69	116	210		
	Cal.	3.3	23.0	68.9	114.8	210	0.512	0.072
Coll. 4	Obs.	3	2	21	24	50		
	Cal.	0.8	5.5	16.4	27.3	50	10.217	1.948
Total ^b	Obs.	15	61	196	369	641		
	Cal.	10.0	70.1	210.3	350.6	641	5.606	2.160
Total of Plant 2 Plus Plant 1	Obs.	15	70	216	401	702		
	Cal.	11.0	76.8	230.3	383.9	702	3.733	

^a Combining the 7-14 and 8-13 classes.

^b For plant 2, using four classes, total $X^2 = 27.295$ (12 D/F) and X^2 for heterogeneity = 21.689 (9 D/F). Combining the 7-14 and 8-13 classes, total $X^2 = 9.055$ (8 D/F) and $X_h^2 = 6.895$ (6 D/F).

exceeded the conventional level of significance ($0.02 > P > 0.01$). Total X^2 and X^2 for heterogeneity for this plant likewise exceeded X^2 for P of 0.01. It is apparent from examination of the data from collections 2 and 4 that the deviations in the 7-14 class are the principal contributors to the high values of X^2 . The difficulty arises from using X^2 when the calculated numbers are small (Fisher 1936). When the data for the 7-14 and 8-13 classes were combined, the fit of observed to calculated was satisfactory as indicated by X^2 for each collection, X^2 for total, total X^2 , and X^2 for heterogeneity (table 3). When the data for plant 1 were combined with those for plant 2 (table 3), there was a total of 702 sporocytes. The fit of the observed ratio to calculated was good ($0.30 > P > 0.20$).

In addition to sporocytes without laggards, data were obtained from 501 anaphase I cells with one laggard (fig. 5), 293 with two, 117 with three, and 23 with four. The values of X^2 for the data from the four collections of plant 2 for the sporocytes with one, two, and three laggards are summarized in table 4. All values of total X^2 , X_1^2 , and X_n^2 gave $P > 0.05$ either when

all classes were used or when the two classes with low calculated frequencies were combined. The fit of observed to calculated also was good in each of the three types of sporocytes when the data from plant 1 were combined with data from plant 2. For sporocytes with one laggard $0.30 > P > 0.20$, for those with two laggards $0.95 > P > 0.90$, and for those with three laggards $0.50 > P > 0.30$.

TABLE 4. Summary of degrees of freedom and values of total X^2 , X^2 for total, and X^2 for heterogeneity obtained from data on anaphase I distribution from four collections of plant 2 for sporocytes with one, two, and three lagging chromosomes.

Number of classes used	Source of X^2	Value of X^2 for sporocytes with indicated number of laggards					
		One		Two		Three	
		D/F	X^{2b}	D/F	X^{2b}	D/F	X^{2b}
All	Total X^2	12	16.017	8	3.605	8	2.761
	X^2 for total	3	3.300	2	0.270	2	0.127
	X^2 for heterogeneity	9	12.717	6	3.335	6	2.634
Combining two classes ^a	Total X^2	8	7.821	4	0.688	4	1.677
	X^2 for total	2	3.258	1	0.166	1	0.007
	X^2 for heterogeneity	6	4.563	3	0.522	3	1.670

^a 7-13 and 8-12 classes for sporocytes with one laggard, 7-12 and 8-11 classes for those with two laggards, and 7-11 and 8-10 classes for those with three laggards.

^b All values of X^2 give $P > 0.10$.

DISCUSSION

The results from metaphase I of triploid *Lolium perenne* are consistent in general with the assumption that the unoriented univalents lie in the microsporocyte at random relative to one another and to the equatorial plate. The single exception was in the sporocytes with three univalents, all unoriented, in which the observed ratio of 1-2 and 0-3 positions deviated from the expected 3:1 by an amount greater than could be attributed to chance more than one or two times in a hundred. Since all other results were consistent with the hypothesis, it seems probable, nevertheless, that the deviation in this one instance may have been due to chance.

The distributions at anaphase I also were consistent with the hypothesis of chance position of the unoriented metaphase I univalents and random assortment of the extra chromosomes of the trivalents. Thus the results from *Lolium perenne* are contrary to those obtained by Satina and Blakeslee (1937a) from triploid *Datura stramonium*. Rather large samples of sporocytes were used in both experiments and, as pointed out by Satina and Blakeslee (1937a), the chances for systematic errors in observation affecting the results obtained seem to be small. Furthermore, the consistency of results within both species seems to rule out the possibility that the differences in

results are due to chance. It is apparent that the assortment of extra chromosomes at anaphase I in *L. perenne* is not like that in *D. stramonium*. It may be questioned, therefore, whether the unexpected behavior in *Datura* may be attributed, as the authors suggested (1937a), to the general nature of chromosomes and the mechanisms involved in their movements at division. Data from other species besides *Datura* and *Lolium* are required before the general problem of assortment of extra chromosomes can be evaluated properly.

SUMMARY

The occurrence and position of univalents at metaphase I and the assortment of chromosomes at anaphase I were studied in microsporocytes from two autotriploid plants of *Lolium perenne* L. In 84 per cent of 2,494 metaphase I sporocytes, from one to five univalents were found. Of these univalents there was one oriented on the equatorial plate in 22 per cent of the sporocytes, two oriented in 7 per cent, three in 0.9 per cent, and four in 0.2 per cent. In sporocytes with two or more unoriented univalents, the univalents lay in the sporocyte at random relative to one another and to the equatorial plate.

The distribution of chromosomes in 1,636 anaphase I sporocytes was consistent with the assumption of chance position of the metaphase I univalents and random assortment of the extra chromosomes of the trivalents. The behavior in triploid *Lolium perenne* differs from that found in triploid *Datura stramonium* by Satina and Blakeslee (1937a, b).

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STUDIES IN ONAGRACEAE—XIII.¹ THE AMERICAN SPECIES OF LUDWIGIA

PHILIP A. MUNZ

It is a pleasure to acknowledge indebtedness to those in charge of the herbaria listed below and to thank them for their kindness in loan of material used in the preparation of this paper: Field Museum, Chicago, Ill. (FM) for special material; Gray Herbarium of Harvard University (GH); New York Botanical Garden (NY); Pomona College (POM); United States National Herbarium (US) for special material.

It is my regret that in this country we do not have ample material of *Ludwigia* from the Old World to warrant my including a treatment of the species occurring there, but under the present world conditions it is impossible to borrow such material.

THE GENUS LUDWIGIA²

Flowers normally 4-merous, the stamens as many as the sepals and with relatively short filaments. Petals often small or lacking; if conspicuous usually early deciduous. Hypanthium not prolonged beyond the ovary; sepals persistent. Summit of ovary truncate or flattish, or crowned with pyramidal to depressed persistent 4-lobed base of style (stylopodium); style short; stigma capitate to somewhat 4-lobed. Capsule subspheric, to obpyramidal, to elongate and angled or subterete, dehiscing by a terminal pore or longitudinally. Seeds numerous, naked with evident raphe and multiseriate in each cell, or rarely enclosed in endocarp and uniseriate. Mostly perennial swamp-plants, with opposite or alternate leaves and solitary axillary flowers or these in terminal spikes or heads.

TYPE SPECIES: *L. alternifolia* L. A genus of about 30 species, largely American, but with a few in the warmer regions of the Old World. Named for C. G. Ludwig (1709-1773), professor in Leipzig. Among the Old World species may be cited:

- (1) *L. palustris*, common to both Old and New Worlds.
- (2) *L. ovalis* Miq. from Japan; of the sect. *Dantia*.
- (3) *L. parviflora* Roxb. of Asia and Africa; it may well be a synonym of *L. perennis* L. 1753, a much earlier name. It surely is the same as *Jussiaea caryophylla* Lam. 1789. It very much resembles *J. erecta*.
- (4) *L. prostrata* Roxb. 1820, for which *L. jussiaeoides* Desr. in Lam. 1789 is an earlier name. It is near to *Jussiaea linifolia* Vahl in its uniseriate seeds, each inclosed in a spongy almost rhomboid endocarp.

From a study of the above species one might conclude that *Ludwigia* was derived from *Jussiaea*, to which it is closely related in its persistent sepals, bracteoles at base of hypanthium, mostly multiseriate ovules, etc., and from

¹ No. XII of this series was published in *Darwiniana* 4: 179-284. 1942.

² For spelling, see Int. rules of bot. nomen., ed. 3, Art. 71(4). 1935.

which it is largely separated by having 4 instead of 8 stamens. It may well have arisen by the suppression of the inner whorl of stamens and have originated in the Old World, *L. perennis* and *L. jussiaeoides* being primitive. Within the genus are tendencies to suppress petals, shorten the fruit, develop a stylopodium, toward opposite and even verticillate leaves, etc.

Synonymy in the genus being well established and for the sake of space, it is omitted here.

KEY TO AMERICAN SPECIES OF LUDWIGIA

A. Leaves opposite to whorled; flowering stems prostrate, creeping or floating, rooting freely.

B. Petals lacking or minute; leaves petioled. (Sect. *Dantia*.³)

TYPE SPECIES: *L. palustris* (L.) Ell.

C. Plants definitely pubescent; bracteoles of hypanthium base not evident.

1. *L. spathulata*.

CC. Plants essentially glabrous; bracteoles usually evident under a lens.

D. Hypanthium and capsule with 4 evident longitudinal green bands and with basal bracteoles not more than 1 mm. long or not evident; petals lacking.

2. *L. palustris*.

DD. Hypanthium and capsule lacking green bands, with bracteoles above the base and 1-5 mm. long; petals present but easily shed.

3. *L. natalans*.

BB. Petals conspicuous; leaves subsessile. (Sect. *Ludwigiantha*.⁴)

TYPE SPECIES: *L. arcuata* Walt.

C. Pedicels usually 15-35 mm. long, exceeding leaves; petals usually 8-10 mm. long, exceeding sepals. So. Car. to Fla.

4. *L. arcuata*.

CC. Pedicels shorter than leaves; petals 1.3-6 mm. long, not exceeding sepals.

D. Leaves opposite. Plants of U. S.

E. Pedicels 5-15 mm. long; sepals 4-6 mm. long. N. J. to So. Car.

5. *L. brevipes*.

EE. Pedicels 1-2 mm. long; sepals 2.5-3 mm. long. R. I. and Conn.

6. *L. lacustris*.

DD. Leaves whorled. Plants of So. Mexico to Panamá.

7. *L. verticillata*.

AA. Leaves alternate; flowering stems erect or ascending.

B. Capsule on a short pedicel and opening by a terminal pore, cubical-spherical; roots fascicled, often fusiform-thickened; stolons lacking. (Sect. *Ludwigia*.⁵)

³ *Dantia*, as sect., DC. Prodr. 3: 61. 1828; as genus, Petit ex L. Gen. ed. 1, 337. 1737. *Danthia* Steud. Nom. ed. 2, 1: 482. 1840. *Isnardia* as sect., Torrey & Gray, Fl. N. Am. 1: 525. 1840; as genus, L. Sp. Pl. 120. 1753. Rather succulent herbs, usually with opposite petioled leaves which are not much reduced up the stems; rooting freely at nodes; stipules minute, triangular, glandlike; flowers minute, solitary in axils; hypanthium oblong-obovoid or turbinate, somewhat 4-sided, with or without basal bracteoles; sepals deltoid; petals present or lacking; capsule more or less corky, septicidal, short, flat at the somewhat 4-lobed apex.

⁴ *Ludwigiantha*, as sect., Torrey & Gray, Fl. N. Am. 1: 526. 1840; as genus, Small, Bull. Torrey Club 24: 177-178. 1897. Stems prostrate or decumbent, creeping or floating; leaves opposite to whorled, sessile or nearly so, numerous, not much reduced up the stems; flowers solitary in leaf-axils, pedicelled, with pair of setaceous bractlets at base of hypanthium; petals conspicuous, but readily shed; filaments widened toward base; capsules usually curved at base, elongate-clavate, with a prominent 4-lobed stylopodium.

⁵ *Ludwigia*, as sect., DC. Prodr. 3: 60. 1828. Sect. *Euludwigia*, Torrey & Gray, Fl. N. Am. 1: 522. 1840; "*Alternifoliae*" of Small, Man. S.E. Fl. 941. 1933. Roots fascicled, more or less fusiform, perennial; stems erect; leaves alternate; petals well developed; stylopodium hairy; capsules pedicelled, opening by a terminal pore on dehiscence of style.

TYPE SPECIES: *L. alternifolia* L.

- C. Plant hirsute; capsules hirsute, shorter than the lance-deltoid sepals which are about 1 cm. long in fruit. 8. *L. hirtella*.
- CC. Plant glabrous or puberulent; sepals ovate to lance-ovate.
- D. Cauline leaves sessile; petals much longer than sepals; pedicel longer than capsule.
- E. Style 7-10 mm. long; leaves glabrous to minutely puberulent under a lens; flowers in axils of bracts less than 1 cm. long. 9. *L. virgata*.
- EE. Style 3-5 mm. long; leaves obviously pubescent, usually to naked eye; flowers borne in axils of bracts 1-2.5 cm. long. 10. *L. maritima*.
- DD. Cauline leaves with short petioles; petals about as long as sepals; pedicel not longer than capsule. 11. *L. alternifolia*.
- BB. Capsule sessile, dehiscing by valves separating from the disk-like top; plants with creeping stolons. (Sect. *Microcarpum*.^a)
- C. Capsule about as long as thick, subspherical to cubic-spherical.
- D. Cauline leaves not spatulate; capsule mostly 3-5 mm. long.
- E. Plant conspicuously pilose; upper leaves subelliptic; flowers somewhat crowded at ends of branches. 12. *L. pilosa*.
- EE. Plant glabrous to puberulent to pubescent in upper parts; upper leaves mostly lance-linear.
- F. Flowers in terminal heads; bractlets at base of hypanthium ovate to elliptic-lanceolate. 13. *L. suffruticosa*.
- FF. Flowers in elongate interrupted leafy spikes; bracteoles mostly more narrow or lacking.
- G. Capsules sharply 4-angled or -winged.
- H. Seeds cylindric, 3-4 times as long as wide; sepals deltoid-ovate, about as wide as long, shorter than the capsule. 14. *L. lanceolata*.
- HH. Seeds ovoid, about twice as long as wide; sepals slightly longer than wide, about as long as capsule. 15. *L. alata*.
- GG. Capsules subglobose, scarcely 4-sided.
- H. Bracteoles at or just above base of hypanthium, 2-5 mm. long; seeds yellowish. 16. *L. polycarpa*.
- HH. Bracteoles if evident less than 1 mm. long; seeds brown. 17. *L. sphacrocarpa*.
- DD. Cauline leaves spatulate or nearly so; capsule 1-3 (4) mm. long.
- E. Capsule 1-1.5 mm. long, shorter than the broad spreading sepals; leaf-blades usually at least half as wide as long. Car. to La., Bahamas, Cuba. 18. *L. microcarpa*.
- EE. Capsule 2-4 mm. long, longer than sepals.
- F. Leaf-blades spatulate-obovate to spatulate, 3-7 mm. wide, about 2-3 times as long.
- G. Capsule 2-2.5 mm. long; leaf-blades mostly at least half as wide as long. Fla., Cuba, Jamaica. 19. *L. Simpsoni*.
- GG. Capsule 3-4.5 mm. long; leaf-blades mostly about one-third as wide as long. Fla. 20. *L. spathulifolia*.

cubic-spherical, perhaps tardily loculicidal; bracteoles well developed at base of hypanthium; base of stem often with considerable aerenchyma but lacking stolons.

^a *Microcarpum* Munz, sect. nov. ('*Microcarpeae*' of Small, Man. S.E. Fl. 941. 1933.) Plantae nostrae fere perennes, cum stolonibus foliosis et postea surculis erectis; foliis alternis; floribus sessilibus axillaribusque, aliquando in spicis aut capitulis confertis; capsula valvis dehiscente, quae ab apice discoideo separant, subspherica aut cubico-spherica aut obpyramidale aut cylindrica. TYPE SPECIES: *L. pilosa* Walt.

- FF. Leaf-blades narrow-spatulate, 1-3 (4) mm. wide, at least 4 times as long; capsule 2.5-3.5 mm. long. Fla. 21. *L. Curtissii*.
 CC. Capsule definitely longer than thick, cylindric to 4-angled.
 D. Petals lacking; bracteoles linear, scarcely 1 mm. long; capsules subcylindric, sometimes slightly 4-grooved. 25. *L. glandulosa*.
 DD. Petals equalling or exceeding sepals, but easily shed.
 E. Capsules subcylindric, not much thickened upward.
 F. Leaves linear, 1-2.5 mm. wide; sepals 4-6 mm. long; capsules 8-9 mm. long. U.S. 22. *L. linifolia*.
 FF. Leaves narrow-spatulate, 2-5 mm. wide; sepals 2 mm. long; capsules 5-7 mm. long. Cuba. 23. *L. stricta*.
 EE. Capsules 4-angled, about twice as thick at summit as at base. U.S. 24. *L. linearis*.

TREATMENT OF SPECIES

1. LUDWIGIA SPATHULATA Torr. & Gray, Fl. N. Am. 1: 526. 1840.

Isnardia spathulata Kuntze, Rev. Gen. 1: 251. 1891; Small, Bull. Torrey Club 24: 177. 1897.

Plant pubescent; stems 1-3 dm. long; leaves rhombic-spatulate to ovate, 1-1.5 (2) cm. long, 3-8 mm. wide, with 4-5 inconspicuous veins on each side of midrib, gradually narrowed into petioles 3-10 mm. long; sepals suborbicular-ovate, 1-1.5 mm. long; petals lacking; capsule globose-obovoid, 3 mm. long.

Type locality: "Middle Florida, Dr. Chapman." *Material seen*, all from Florida: without definite locality, Chapman (GH); Gadsden Co., Chapman in 1835 (NY); Walton Co., De Funiak Springs, Curtiss 6853 (GH, NY).

2. LUDWIGIA PALUSTRIS (L.) Elliott, Sketch Bot. S. Car. & Ga. 1: 211. 1821.

Isnardia palustris L. Sp. Pl. 120. 1753.

Nearly or quite glabrous, succulent; leaves lanceolate to elliptic-ovate, the blades 3-25 mm. long, on petioles 3-20 (25) mm. long; flowers sessile, axillary; hypanthium usually with 4 longitudinal green bands; capsule somewhat corky, oblong-obovoid, somewhat 4-sided, rounded at base, truncate at apex, 2-5 mm. long, 1.4-3.5 mm. thick.

The var. *typica* Fernald & Griscom (Rhodora 37: 176. 1935) is characterized by having the green bands on the hypanthium terminating well below the summit. It occurs in Europe, Africa, and western Asia. The American varieties were recently thoroughly treated by Fernald and Griscom (Rhodora 37: 176) and for sake of space do not need consideration here. They may be keyed as follows:

- A. Leaf-blades usually at least half as wide as long; capsules 2-3.5 mm. thick. Atlantic Coast to Cascade Mts. and Sierra Nevada; occasional to Central America. var. *americana* (DC.) Fern. & Griscom.
 AA. Leaf-blades one-third to one-fourth as wide as long.
 B. Leaf-blades mostly less than 1 cm. long; capsules less than 2 mm. thick. Southern U.S. to Colombia. var. *nana* Fern. & Griscom.
 BB. Leaf-blades mostly more than 1 cm. long; capsules 2-2.8 mm. thick. Brit. Columbia to Calif. west of the mts. var. *pacifica* Fern. & Griscom.

3. LUDWIGIA NATANS Elliott, Sketch Bot. S. Car. & Ga. 1: 581. 1821.

Much like *L. palustris*, but leaf-blades 5–45 mm. long, 3–30 mm. wide, rhombic-ovate to almost orbicular-ovate or -obovate; flowers sessile or short-pedicelled; hypanthium lacking green bands, and with more evident bractlets; capsule 3–8 mm. long.

Key to Varieties of *L. natans*

A. Fruits 3–5 (6) mm. long, sessile or on pedicels up to 1 mm. long; bracteoles mostly 1–3 mm. long; petioles mostly 3–10 mm. long. Carolina to Missouri, Texas, Cuba, Bermuda. var. *typica* Fern & Griscom.

AA. Fruits 6–8 mm. long; bracteoles mostly 2–5 mm. long; petioles 5–20 mm. long.

B. Fruits sessile, mostly 2–2.5 mm. thick. Atlantic Coast of U.S. to Rocky Mts. and West Indies. var. *rotundata* (Griseb.) Fern. & Griscom.

BB. Fruits on pedicels 2–4 mm. long and mostly 3–3.5 mm. thick. S. Calif. var. *stipitata* Fern. & Griscom.

Since this species was also recently treated by Fernald & Griscom, *Rhodora* 37: 175. 1935, I shall omit further discussion here.

4. LUDWIGIA ARCUATA Walt. Fl. Car. 89. 1788.

Isnardia arcuata Kuntze, Rev. Gen. 1: 251. 1891. *Ludwigiantha arcuata* Small, Bull. Torrey Club 24: 178. 1897. *Ludwigia pedunculosa* Michx. Fl. Bor. Am. 1: 88. 1820. *Isnardia pedunculosa* DC. Prodr. 3: 60. 1828.

Fleshy, subglabrous to strigulose, the creeping stems 5–25 cm. long; leaves rather crowded, the blades oblanceolate to elliptic-linear, 8–20 mm. long, 1–2.5 mm. wide, sessile or nearly so; pedicels 15–35 mm. long; bracteoles 1–3 mm. long; hypanthium elongate-funnelform; sepals linear-lanceolate, spreading, acuminate, 4–8 mm. long; petals 6–10 mm. long; capsule clavate-oblong, somewhat arcuate at base, 6–8 mm. long, 2–3 mm. thick, somewhat 4-sided.

Type locality: Carolina; range from South Carolina to Florida. *Represented by*: S. CAROLINA: Charleston Co., near Charleston, *Ravenel* (GH). GEORGIA: Chatham Co., Savannah, *Canby in 1869* (GH, NY). FLORIDA: Leon Co., Jackson Lake, *Wiegand & Manning 2182* (GH, POM); Jefferson Co., Lloyds, *Nash 2509* (GH, NY); Lake Co., Eustis, *Nash 607* (GH, NY); Hillsborough Co., Tampa, *Curtiss 934* (GH, NY).

5. LUDWIGIA BREVIPES (Long) E. H. Eames, *Rhodora* 35: 228. 1933.

Ludwigiantha brevipes Long, in Britton & Brown, Ill. Fl. ed. 2, 2: 586. 1913.

Leaves 2–6 mm. wide; pedicels 5–15 mm. long; petals 4–6 mm. long; capsule clavate, 7–10 mm. long.

Type locality: Little Egg L. S. S., Long Beach Island, Ocean Co., New Jersey. Ranging south to S. Carolina. *Represented by*: Long 173, type coll. (GH, NY). VIRGINIA: Fernald & Long 8376 (GH, NY, POM); Fernald & Long 4070 (GH, NY). N. CAROLINA: Godfrey 5247 (GH). S. CAROLINA: Godfrey & Tryon 1195 (GH, NY, POM).

6. LUDWIGIA LACUSTRIS E. H. Eames, *Rhodora* 35: 228. 1933.

L. lacustris f. *aquatilis* Eames, *Rhodora* 35: 229. 1933.

Like the preceding, but with pedicels 1–2 mm. long; petals 1.3–3 mm. long; capsules about 5 mm. long.

Type locality: Watchaug Pond, Charleston, Washington Co., R. I. Type seen, also collections from CONNECTICUT: New Haven Co., Guilford, *Eames* 11473, 11474a, 11475, 11476 (GH); New London Co., Old Lyme, *Eames* 11496, 11494, 11495 (GH); Lyme, *Eames* 11460 (GH).

7. *Ludwigia verticillata* Munz, sp. nov.

Caules tenues, 1–2 mm. crassi, subglabri, virides, cum ramis decumbentibus aut ascendentibus, 3–15 cm. longis; internodiis 2–8 mm. longis; foliis numerosis, verticillatis (3, 4, ad 6), anguste elliptico-oblongatis, 8–18 mm. longis, 1–3 mm. latis, in extremis ambobus acutis, subintegris, glabris, cum petiolis 1–2.5 mm. longis, laminis cum 7 venis principalibus in latere quoque; floribus paucis, in axillis superioribus solitariis; pedicellis 1.5–3 mm. longis; bracteolis vix evidentibus; hypanthio glabro, clavato-subcylindrico, in anthesi 5–6 mm. longo; sepalis deltoideo-ovatis, 2.5–4 mm. longis, 1.5–2 mm. latis, subobtusis, 3–5-venatis; petalis 4–5 mm. longis et latis; staminibus 1.5–2.5 mm. longis; filamentis base latis; antheris circa 0.7 mm. longis; stylopodio depresso, piloso; stylo crasso, ca. 2 mm. longo; stigmatibus 1 mm. crasso; capsula glabra, 7–8 mm. longa, 1.5–2 mm. crassa, vix 4-angulata, cum stria mediana in superficie quoque; seminibus in serie una indefinita in loculo quoque, subovoideis, ca. 0.6 mm. longis, ferrugineis, nitidis.

TYPE: Laguna de Portola, near Chepo, province of Panamá, Panamá, at 50 m. alt., *H. Pittier* 4605, Oct., 1911, U. S. Nat. Herb. no. 679760. Other collections seen: HONDURAS: Amapala, Isla Tigre, *Standley* 20771 (US). MEXICO: "Acapulco and vicinity," *Palmer* 577 (US).

In general appearance, elongate fruit, broad filaments and evident petals near to *L. lacustris*, *L. brevipes*, etc., but distinct in its whorled leaves, seeds seemingly in 1 row, stylopodium less prominent and hairy, reduced bracteoles, and southern range.

8. *LUDWIGIA HIRTELLA* Raf. Med. Rep. N. Y. 5: 358. 1808.

Isnardia hirtella Kuntze, Rev. Gen. 1: 251. 1891. *L. pilosa* Elliott, Sketch Bot. S. Car. & Ga. 1: 216. 1821, not Walter, 1783. *L. permollis* Barton, Fl. Virg. 1: 52. 1812, from description. *L. hirsuta* Pursh, Fl. Am. Sept. 1: 110. 1814, not Desr. 1789. *Isnardia hirsuta* R. & S. var. *permollis* DC. Prodr. 3: 60. 1828.

Erect, 3–9 dm. high, hairy; leaves sessile, lance-oblong to ovate-oblong, hirsute, 2–5 cm. long, 0.5–1.2 cm. wide, gradually reduced upward; pedicels 3–8 mm. long; bracteoles 3–4.5 mm. long; sepals 7–10 mm. long; petals 10–15 mm. long; capsule subglobose-cubical, hirsute, green at the prominent angles, 4–6 mm. long; seeds 0.6 mm. long.

Type locality: Baltimore, Md. Range along the coast from New Jersey to northern Florida, and eastern Texas. For sake of space citation of specimens is omitted.

9. *LUDWIGIA VIRGATA* Michx. Fl. Bor. Am. 1: 89. 1803.

Isnardia virgata DC. Prodr. 3: 60. 1828.

Stems simple or few-branched, fine-puberulent to glabrous, 3–8 dm. high; leaves sessile, not crowded, lowermost oblong, 1–3 cm. long, principal ones

oblong-lanceolate to oblong-linear, 3–6 (8) cm. long, 3–7 mm. wide, gradually reduced up the stem to oblong-linear bracts 5–8 mm. long; leaves subglabrous to puberulent; flowers in terminal spicate racemes; pedicels 6–10 (15) mm. long; bracteoles 2–5 mm. long; sepals reflexed, 6–11 mm. long, 3.5–4.5 mm. wide, lance-deltoid; petals 10–15 mm. long; style 7–10 mm. long; stigma 2 mm. thick; capsule subglobose-spherical, 5–6 mm. long, almost winged at the sharp angles; seeds light brown, shining, 0.6–0.7 mm. long.

Type locality: S. Carolina. Ranging along the coast from North Carolina to northern Florida. Much material which has been referred here belongs to *L. maritima*. *Representative of L. virgata*: N. CAROLINA: New Hanover Co., Wilmington, *Biltmore Herb.* 4168 (GH, NY); Moore Co., Pine Bluff, *Wiegand & Manning 2203* (GH); Columbus Co., Bolton, *Wiegand & Manning 2204* (GH, POM). S. CAROLINA: Williamsburg Co., Kingstree, *Wiegand & Manning 2205* (GH, POM); Salters, *Godfrey & Tryon 523* (GH, NY, POM); Charleston Co., McClellanville, *Godfrey & Tryon 1132* (GH, NY, POM). GEORGIA: Ware Co., Suwanee Lake, *Harper 272* (GH, NY). FLORIDA: Wakulla Co., St. Marks, *Rugel in 1843* (NY); Duval Co., Jacksonville, *Curtiss 919* (GH, NY).

10. LUDWIGIA MARITIMA Harper, Torrey 4: 163. 1904.

Like the preceding, but more definitely and evidently pubescent throughout, with hairs up to 0.5 mm. long; upper bract-like leaves 1–2.5 cm. long; bracteoles 2–3.5 mm. long; sepals 5–9 mm. long; petals 9–12 mm. long; style 3–5 mm. long; stigma 1–1.5 mm. thick; capsule 6–8 mm. long.

Type locality: Cumberland Island, Camden Co., Ga. In pine lands from coastal N. Carolina to southern Florida and eastern Louisiana. *Representative collections*: N. CAROLINA: Craven Co., *L. F. & F. R. Randolph 549* (GH). S. CAROLINA: Georgetown Co., Georgetown, *Godfrey & Tryon 786* (GH, NY, POM). GEORGIA: Camden Co., Cumberland I., type coll. *Harper 1542* (FM, GH, NY). FLORIDA: Duval Co., Jacksonville, *Curtiss 4912* (GH, NY). Brevard Co., Okeechobee region, *Fredholm 5996* (GH, NY). Lake Co., Eustis, *Nash 750* (GH, NY). Manatee Co., Bradentown, *Tracy 7087* (GH, NY). Dade Co., Cutler, *Small, Mosier & Small 6702* (GH, NY). ALABAMA: Mobile Co., near Mobile, *Munz 13353* in part (POM); *Baker 850* (NY). MISSISSIPPI: Harrison Co., Biloxi, *Baker in 1897* (NY, POM); Jackson Co., Ocean Springs, *Pollard 1112* (GH, NY, POM). LOUISIANA: St. Tammany Parish, Slidell, *Munz 13347* in part (NY, POM), *13346* (POM).

11. LUDWIGIA ALTERNIFOLIA L. Sp. Pl. 118. 1753.

Plant 4–12 dm. tall; leaves rather crowded, with petioles 3–10 mm. long and principal leaf-blades 4–8 (12) cm. long; pedicels 2–5 mm. long; bracteoles 1–2.5 mm. long; sepals 7–10 mm. long; petals 8–10 mm. long; capsule cubic with rounded base, slightly wing-angled, mostly 5–6 mm. long.

11a. L. ALTERNIFOLIA L. var. *typica* Munz, var. nov.

L. alternifolia L. Sp. Pl. 118. 1753. *Isnardia alternifolia* DC. Prodr. 3: 60. 1828. *L. ramosissima* Walt. Fl. Car. 89. 1788? *L. angustifolia* β *ramosissima* Poir. in Lam. Encycl. Suppl. 3: 513. 1813. *L. macrocarpa* Michx. Fl. Bor. Am. 1: 89. 1803. *L. aurantiaca* Raf. Med. Rep. N. Y. 5: 358. 1808? *Isnardia aurantiaca* DC. Prodr. 3: 61. 1828? *Ludwigia uniflora* Raf. Med. Rep. N. Y. 5: 358. 1808? *Isnardia alternifolia* γ *uniflora* DC. Prodr. 3: 60. 1804? *L. salicifolia* Poir. in Lam. Encycl. Suppl. 5: 512. 1813. *Isnardia alternifolia* β *salicifolia* DC. Prodr. 3: 60. 1804. *L. microcarpa* Link. Enum. Hort. Berol. 141. 1821. *Rhexia linearifolia* Poir. in Lam. Encycl. 6: 2. 1804? *Ludwigia alternifolia* var. *linearifolia* Britton, Bull. Torrey Club 17: 315. 1890.

Plant subglabrous or more or less strigulose on stems, pedicels and leaves.

Type locality: "Habitat in Virginia." Very common and ranging from Massachusetts to northern Florida, Ontario, Iowa, and Louisiana. Intergrading with the following variety; some specimens, especially from the southern and western parts of the range becoming more pubescent, although the hairs may be quite appressed.

11b. *L. ALTERNIFOLIA* L. var. *PUBESCENS* Palmer & Steyermark, Ann. Mo. Bot. Gard. **25**: 772. 1938.

Stems, leaves, pedicels, and capsules densely pubescent with erect hairs.

Type locality: 4 miles west of Charleston, Mississippi Co., Mo., the TYPE being Palmer & Steyermark 41450. Other collections seen: INDIANA: Deam 41713. ILLINOIS: Waite 1177. KANSAS: Norton 155, Rydberg & Imler 404. ARKANSAS: Demaree 17767, 19907, 20064, 20149, 15612, 19793, etc. LOUISIANA: Hale, Drummond, Palmer 8012, Ball 617. TEXAS: Wright, Lindheimer 69, Cory 25300.

12. *LUDWIGIA PILOSA* Walt. Fl. Car. 89. 1788.

Isnardia pilosa Kuntze, Rev. Gen. 1: 251. 1891. *Ludwigia rudis* Walt. Fl. Car. 89. 1788. *L. hirsuta* Desr. in Lam. Encycl. 3: 614. 1789. *I. hirsuta* R. & S. Syst. 3: 477. 1818, as to name and in part as to concept; DC. Prodr. 3: 60. 1828. *L. mollis* Michx. Fl. Bor. Am. 1: 90. 1803. *I. mollis* Poir. in Lam. Encycl. Suppl. 3: 188. 1813. *L. capitata* var. *pubens* Torr. & Gray, Fl. N. Am. 1: 525. 1840.

Stoloniferous at base, the main stems soon erect, 5–12 dm. high, pilose; leaves of stolons orbicular- to oblong-ovate, with blades 8–16 mm. long, petioles 5–8 mm. long; cauline leaves oblong-lanceolate to elliptic to linear-lanceolate, petioles 1–5 mm. long, blades 2–10 cm. long, reduced up the stem; flowers usually crowded toward ends of branches; bracteoles 3–4 mm. long; sepals 4–5 mm. long; petals apparently lacking; capsules sessile, cubic-globose, somewhat 4-sided but not sharply angled, 3–4 mm. long.

Type locality: Carolina. Range along coast from southern Virginia to Florida and eastern Texas.

13. *LUDWIGIA SUFFRUTICOSA* Walt. Fl. Car. 90. 1788.

Isnardia suffruticosa Kuntze, Rev. Gen. 1: 251. 1891. *Ludwigia capitata* Michx. Fl. Bor. Am. 1: 90. 1803. *Isnardia capitata* DC. Prodr. 3: 60. 1828.

Stolons pubescent, with almost sessile leaves; main stems glabrous, the main leaves sessile, linear-lanceolate to lanceolate, 3–8 (10) cm. long; flowers in subcapitate spikes; pedicels less than 1 mm. long; bracteoles 3 mm. long; sepals 2.5–3 mm. long; petals not seen; capsule broadly obpyramidal, somewhat quadrangular but rounded at angles, 3.5–4 mm. long, slightly thicker.

Type locality: Carolina. Ranging along coast from N. Car. to south central Fla.

14. *LUDWIGIA LANCEOLATA* Elliott, Sketch Bot. S. Car. & Ga. 1: 213. 1821.

Isnardia lanceolata DC. Prodr. 3: 61. 1825.

Leaves of stolons elliptic- to rhombic-obovate or narrower, 1.5–3 cm. long, short-petioled; principal cauline leaves oblanceolate to linear-lanceolate, 2–8

(10) cm. long, 2–8 (11) mm. wide, sessile or on petioles a few mm. long; flowers almost sessile, in spikes several cm. long; bracteoles 2–3 mm. long; sepals deltoid-ovate, abruptly acute, 3 mm. long; petals none; capsules obpyramidal, almost winged at the sharp angles, 4–4.5 mm. long, about as thick; seeds cylindric, about 0.7 mm. long, one-third to one-fourth as thick.

Type locality: "swamps of Georgia"; much confused with the next species. *Representative collections*: GEORGIA: swamps, Baldwin, type at Elliott Herbarium (photo POM); Harper 1605 and 1483. FLORIDA: *Biltmore Distribution* 4177, Nash 2502, Rugel 245, Curtiss 927, Fredholm 5987, Small & Carter 2627.

15. LUDWIGIA ALATA Elliott, Sketch Bot. S. Car. & Ga. 1: 212. 1821.

Isnardia alata DC. Prodr 3: 61. 1828. *Ludwigia simulata* Small, Fl. S. E. U. S. 816, 1335. 1903.

Like the preceding, but leaves of stolons perhaps more round; sepals deltoid, about 3 mm. long, connate at very base, abruptly subacuminate, somewhat denticulate; capsule 3–4 mm. long; seeds ovoid, about 0.6 mm. long and half as thick.

Type locality: Sullivan's Island, Charleston Co., S. C. Ranging along coast from southeastern Virginia to Florida and Mississippi. *Representative collections*: VIRGINIA: Fernald, Long and Fogg 4960, and 13981 and 13982. N. CAROLINA: Lewis 196, Godfrey & Tryon 718. GEORGIA: Harper 1554. FLORIDA: Rugel in 1843, Curtiss 929, Wiegand & Manning 2172, Hitchcock 113, Small & Carter 1243 and 2624. MISSISSIPPI: Lloyd & Tracy 230 and 6415.

16. LUDWIGIA POLYCARPA Short & Peter, Transylv. Jour. Med. 8: 581. 1835; ex Torrey & Gray, Fl. N. Am. 1: 525. 1840.

Isnardia polycarpa Kuntze, Rev. Gen. 1: 251. 1891.

Leaves on stolons crowded, oblanceolate, 1–2.5 cm. long, those on main stems narrowly lanceolate to oblanceolate, 3–12 cm. long, with winged petioles 2–8 mm. long; flowers sessile; bractlets 2–5 mm. long; sepals 2.5–3.5 mm. long; capsule subglabrous, turbinate, scarcely 4-sided, 3.5–5 mm. long, 3–3.5 mm. thick; seeds yellowish, somewhat punctate under a lens.

Type locality: Kentucky. Moist places, Massachusetts and Connecticut, Ontario to Tennessee and Kansas. Not easily confused with other species.

17. LUDWIGIA SPHAEROCARPA Elliott, Sketch Bot. S. Car. & Ga. 1: 213. 1821.

Isnardia sphaerocarpa DC. Prodr. 3: 61. 1828.

Leaves of stolons elliptic-lanceolate to spatulate-obovate, 1–2 cm. long, principal cauline leaves lanceolate to lance-oblong, 2–10 (12) cm. long, 3–8 (10) mm. wide, sessile or with petioles to 7 mm. long; flowers sessile; bracteoles not more than 1 mm. long; sepals 2.5–3 mm. long; capsule subglobose, 2.5–4.5 mm. long, pubescent to glabrous.

Key to varieties of *L. sphaerocarpa*

- A. Fruit crowded on branches, 3.5–4.5 mm. long, not so wide. Massachusetts to New Jersey. 17c. var. *macrocarpa*.
 AA. Fruit not crowded on branches, 2.5–3.2 mm. long, usually wider.
 B. Main stems and leaves usually glabrous; main leaves linear-lanceolate and more than 7 cm. long. R. I. to Fla. 17a. var. *typica*.
 BB. Main stems and leaves pubescent to strigose, lanceolate, usually less than 7 cm. long. N. J. to Va., Mich., Ind. 17b. var. *jungens*.

17a. *L. SPHAEROCARPA* Elliott var. *TYPICA* Fernald & Griscom, *Rhodora* **37**: 174. 1935.

Since this and the following varieties were amply discussed in 1935 and many specimens were cited, I shall not repeat the material here.

17b. *L. SPHAEROCARPA* L. var. *JUNGENS* Fernald & Griscom, *Rhodora* **37**: 174. 1935.

L. sphaerocarpa var. *Deamii* Fernald & Griscom, *Rhodora* **37**: 174. 1935.

In my opinion the var. *Deamii* was based on inadequate material; other collections than the type and from the same region do not bear out its characters. Var. *typica* and var. *jungens* intergrade freely.

17c. *L. SPHAEROCARPA* L. var. *MACROCARPA* Fernald & Griscom, *Rhodora* **37**: 174. 1935.

New Jersey material is sometimes difficult to distinguish from var. *typica*.

18. *LUDWIGIA MICROCARPA* Michx. Fl. Bor. Am. **1**: 88. 1803.

Isnardia microcarpa Poir. in Lam. Encycl. Suppl. **3**: 188. 1813. *Ludwigia glandulosa* Pursh, Fl. Am. Sept. **1**: 111. 1814, not Walter, 1788.

Creeping at base, the erect stems slender, 1–6 dm. high; leaves of main stems obovate-spatulate to spatulate, 7–25 mm. long, 4–10 mm. wide, with petioles 1–4 mm. long; flowers sessile, solitary; bracteoles 0.5–1.5 mm. long; sepals orbicular-ovate, 1–2 mm. long; petals none; capsule obpyramidal with rounded corners, 1–1.5 mm. long, 1.5–2 mm. thick at summit.

Type locality: South Carolina. Near the coast from N. Carolina to southern Florida and Louisiana; reported also from Tennessee, Missouri, Bahamas, and Cuba. Often difficult to distinguish from some of the following species; *representative material* is cited: NORTH CAROLINA: Carteret Co., Beaufort, *Lewis* 197 (NY). So. CAROLINA: Horry Co., Myrtle Beach, *Godfrey & Tryon* 1163 (GH, NY, POM); Georgetown Co., near Georgetown, *Godfrey & Tryon* 1043 (GH, NY, POM). GEORGIA: Sumter Co., *Harper* 471 (GH, NY). FLORIDA: Duval Co., Jacksonville, *Curtiss* 930 (NY), *Wiegand & Manning* 2188 (GH, POM); Palm Beach Co., Jupiter, *Curtiss* 5545 (NY); Dade Co., Florida City, *O'Neill* 7598 (NY, POM); near Cutler, *Small & Carter* in 1903 (NY). MISSOURI: Oregon Co., Greer, *Steyermark* 27987 (GH, POM). BAHAMAS: Great Bahama, *Brace* 3519 (NY). CUBA: La Magdalena, Cayamas, *Baker* 4648 (POM); La Puntada la Jaula, *Wright* 2554 (GH).

19. *LUDWIGIA SIMPSONI* Chapman, Fl. S. U.S., ed. 2, 2d Suppl. 685. 1892.

L. cubensis Helwig, Fedde Rep. **25**: 53. 1928! Type not seen.

Main leaves spatulate-obovate, 5–15 mm. long, 3–7 mm. wide; petioles 1–3 mm. long; bracteoles 1–2 mm. long; sepals 1.5–2 mm. long; capsule 2–2.5 mm. long, almost as wide, obscurely angular.

Type locality: Manatee, Manatee Co., Fla. Ranging from Wakulla Co., Fla. to Dade Co. and in Cuba and Jamaica. *Representative material*: FLORIDA: Wakulla Co., St. Marks, *Rugel in 1843* (NY); Alachua Co., near Waldo, *Wiegand & Manning 2189* (GH, POM); Orange Co., Sanford, *Nash 2278* (GH, NY); Manatee Co., Manatee, *Simpson*, type coll. (GH, photo POM), *Tracy 7602* (GH, NY); Lee Co., Ft. Myers, *Hitchcock 117* (GH, NY); Palm Beach Co., Jupiter, *Curtiss 5545* (GH, NY, POM); Monroe Co., Pine Key, *Blodgett* (GH, NY); Dade Co., Camp Jackson, *Small & Wilson 1808* (NY). CUBA: Isle of Pines, San Juan, *Britton, Britton & Wilson 15527* (GH, NY). JAMAICA: Black River, *Harris 9935* (NY).

20. *LUDWIGIA SPATHULIFOLIA* Small, Man. Southeast. Fl. 943, 1506. 1933. Published without Latin diagnosis, but valid according to Rules, because of date.

Main leaves spatulate, denticulate toward apex, 1–1.5 cm. long, 3–6 mm. wide, with poorly defined winged petioles 2–9 mm. long; bracteoles 2–2.5 mm. long; sepals 2 mm. long; capsule 3–4.5 mm. long, almost as wide at apex, somewhat rounded at angles.

Type locality: Everglades, northwest of Perrine, Dade Co., Fla. *Material seen*: FLORIDA: Lee Co., Ft. Myers, *J. Standley 76* in part (GH, NY); Dade Co., Royal Palm Hammock, *Small, Mosier & Small 6644* (GH, NY); near Perrine, *Small & Carter 2990*, type no. (NY); Humbugus Prairie, *Small & Mosier 5610* (NY); Camp Jackson, *Small & Wilson 1848* (NY).

21. *LUDWIGIA CURTISSII* Chapman, Fl. S. U. S., Suppl. 621. 1883.

Main leaves oblanceolate-spatulate, denticulate at apex, 1–1.5 cm. long, 1–4 mm. wide, with winged petioles 1–5 mm. long; bracteoles about 2 mm. long; sepals deltoid-lanceolate, 2–2.5 mm. long; capsule 2.5–3.5 mm. long, about as wide.

Type locality given as "East Florida (*Curtiss*)," the *Curtiss* distribution no. 922 on which the labels say "Ludwigia Curtissii, Chapm. n.sp." coming from "Ponds near Cape Malabar, Florida," which I take to be the type locality. *Material seen* all from pine-lands of southern FLORIDA: Manatee Co., Bradentown, *Cuthbert 1364* (NY); Indian River Co., Felsmerc, *Small 8884* (NY); Cape Malabar, *Curtiss 922*, type no. (GH, NY, photo POM); Lee Co., Myers, *Hitchcock 115* (GH, NY); Chapin, *Hitchcock 116* (GH, NY); Monroe Co., Pine Crest, *Moldenke 856a* (NY); Dade Co., near Miami, *Small 4023* (NY).

22. *LUDWIGIA LINIFOLIA* Poir. in Lam. Encycl. Suppl. 5: 513. 1813.

Isnardia linifolia Kuntze, Rev. Gen. 1: 251. 1891.

Leaves of stolons elliptic-obovate to oblanceolate 5–13 (15) mm. long; main cauline leaves linear, acute, sessile, 1–3.5 cm. long, 1–2.5 mm. wide; flowers rather crowded, sessile; bracteoles 1.5–3 mm. long; sepals lance-linear, 4–6 mm. long; petals narrow-obovate, 4–6 mm. long; capsule sub-cylindric, 8–9 mm. long, 1.5 mm. thick, with somewhat corky wall.

Type locality: "croît dans l'Amérique septentrionale." Found in pine-barrens from North Carolina to Florida and Mississippi. *Represented by*: N. CAROLINA: *Godfrey 6195*.

GEORGIA: *Harper 646* and *1109*. FLORIDA: *Wiegand & Manning 2186*, *Curtiss 922*, *4322*, *Nash 1240*, *Fredholm 5378*, *5737*, *Hitchcock 119*, ALABAMA: *Harper 3805*. MISSISSIPPI: *Lloyd & Tracy 225*.

23. *LUDWIGIA STRICTA* Wright ex Sauvalle, Fl. Cubana 54. 1873.

Isnardia stricta Wright ex Griseb. Cat. Pl. Cub. 107. 1866.

Leaves of stolons elliptic-spatulate, 5–8 mm. long, the principal cauline ones oblance-spatulate, 1–2 cm. long, 2–5 mm. wide; bracteoles scarcely 1 mm. long; sepals deltoid-ovate to -lanceolate, about 2 mm. long; petals 3–5 mm. long; capsule subterete, 5–7 mm. long, 1–2 mm. thick.

Type locality not stated; the Wright specimen at Gray Herb. says *Lagunas Vuelotalago*, so far as I can read it. *Material seen* of the species: CUBA: *Wright 2555*, type no. (GH); Piñar del Río, near Herradura, *Britton, Britton, Earle & Gager 6618* (NY); near Piñar del Río, *Britton, Britton and Gager 7233* (NY).

24. *LUDWIGIA LINEARIS* Walter, Fl. Car. 89. 1788.

Leaves of stolons obovate to elliptic, about 1 cm. long; main cauline leaves linear to linear-elliptic, 2.5–6 cm. long, 1.5–5 mm. wide, sessile; flowers sessile in uppermost axils, from few to about a dozen per branch; bracteoles 1–3 mm. long; sepals lance-deltoid, glabrous to puberulent, 2.5–4 mm. long; petals 3.5–5 mm. long; capsule elongate obpyramidal, 6–8 mm. long, about 3 mm. thick.

24a. *L. LINEARIS* Walt. var. *typica* Munz, var. nov.

L. linearis Walt. Fl. Car. 89. 1788. *Isnardia linearis* DC. Prodr. 3: 60. 1828. *Ludwigia angustifolia* Michx. Fl. Bor. Am. 1: 88, 1803.

Stems and leaves glabrous or somewhat strigulose on veins, etc.; hypanthium and sepals minutely granular-strigulose.

Type locality: Carolina. Found in moist places, mostly in pine-barrens from New Jersey to Florida, Tennessee, and eastern Texas. Western material gradually becomes more strigulose and passes into

24b. *L. LINEARIS* var. *PUBERULA* Engelm. & Gray, Pl. Lindh. 9 (Boston Journ. Nat. Hist. 5). 1845.

Whole plant rather densely and closely puberulent.

Type locality: Houston, Texas. Ranging from Mississippi and so. Arkansas to eastern Texas. *Represented by*: MISSISSIPPI: Smith Co., Taylorville, *Tracy 8715* (GH, NY). ARKANSAS: Ashley Co., Mist, *Demaree 18040* (NY, POM). TEXAS: Newton Co., near Deweyville, *Cory 10904* (GH); Hardin Co., Silsbee, *Cory 19965* (GH); Waller Co., Hempstead, *E. Hall 221* in part (NY, POM); Harris Co., Houston, *Lindheimer 58*, type no. (GH); Brazoria Co., Columbia, *Bush 1542* (GH, NY).

25. *LUDWIGIA GLANDULOSA* Walt. Fl. Car. 88. 1788.

Leaves of stolons elliptic-ovate to -obovate, the blades 1–2 cm. long, petioles 5–10 mm. long; main cauline leaves mostly lanceolate, the blades 3–10 cm. long, 6–20 mm. wide, on petioles 3–10 mm. long; bracteoles scarcely 1 mm. long; sepals deltoid to almost lanceolate, 1–2 mm. long; petals none;

capsules sessile, subcylindric, sometimes 4-grooved, 2–8 mm. long, 1.5–2 mm. thick.

25a. *L. GLANDULOSA* Walt. var. *typica* Munz, var. nov.

L. glandulosa Walt. Fl. Car. 88. 1788. *L. cylindrica* Elliott, Sketch Bot. S. Car. & Ga. 1: 213. 1817. *Isnardia cylindrica* DC. Prodr. 3: 60. 1828. *Jussiaea brachycarpa* Lam. Encycl. 3: 331. 1789. *Ludwigia heterophylla* Poir. in Lam. Encycl. Suppl. 3: 512. 1813.

Hypanthium and sepals mostly quite glabrous; sepals 1.5–2 mm. long; capsule 6–8 mm. long.

Type locality: Carolina. Ranging from Virginia to northern Florida and the Gulf states, and from southern Illinois and Indiana to eastern Texas.

25b. *L. GLANDULOSA* Walt. var. *Torreyi* Munz, nom. nov.

L. cylindrica Ell. β *brachycarpa* Torrey & Gray, Fl. N. Am. 1: 524. 1840; not *Jussiaea brachycarpa* Lam. Encycl. 3: 331. 1789.

Hypanthium and sepals minutely strigulose; sepals 1–1.5 mm. long; capsules 2–4 mm. long.

So far as I can determine, Torrey & Gray had in mind Lamarek's name *brachycarpa* for their variety, but I have seen a photograph of his type and it is long-fruited. They cited a Chapman collection from Florida and one by E. Hall, no. 219, from Hempstead, Texas. Since this has a definite locality, I propose it be taken as the type collection.

This variety is represented by: FLORIDA: without definite locality, *Chopman* (NY). LOUISIANA: *Cameron*, *Tracy 8496* (GH, NY). TEXAS: *Dallas*, *Reverchon* (GH, NY); *Robertson Co.*, *College Station*, *Reverchon 2000* (NY); *Brazos Co.*, *Wellborn*, *Reeves 938* (POM); *Brazoria Co.*, *Bush 1399* (NY).

UNCERTAIN AND EXCLUDED SPECIES OF LUDWIGIA

- L. angustifolia* (Lam.) Gomez, An. Hist. Nat. Madrid 23: 66. 1894 is *Jussiaea suffruticosa* var. *ligustrifolia* (HBK.) Griseb.
- L. Bertonii* Lévl. in Bertoni, Descr. Fis. Econ. Parag. 3: 1910 may be a *Jussiaea*.
- L. brachycarpa* DC. Prodr. 3: 55. 1828, in obs., is probably *Jussiaea brachycarpa* Lam., hence *L. glandulosa* Walt. var. *typica*.
- L. Clavellina* var. *grandiflora* Gomez, l. c. is *Jussiaea uruguayensis* Camb.
- L. Clavellina* var. *peplodes* Gomez, l. c. is *Jussiaea repens* var. *peplodes* (HBK.) Griseb.
- L. decurrens* Walt. Fl. Car. 89. 1788 is *Jussiaea decurrens* (Walt.) DC.
- L. diffusa* Greene var. *californica* Greene, Fl. Francisc. 227. 1891 is *Jussiaea repens* var. *peplodes* (HBK.) Griseb.
- L. foliosa* Gomez, l. c. is *J. leptocarpa* var. *angustissima* Helwig.
- L. hastata* Spreng. Syst. 1: 446. 1825 (*Isnardia hastata* R. & P. Fl. Peruv. 1: 66, pl. 85, f. 6. 1798) is *Ammania latifolia* L. acc. Kew Index.
- L. hirta* Gomez, l. c. is *Jussiaea peruviana* L.
- L. hondurensis* Standl. Field Mus. Pub. Bot. 8: 146. 1930 is *Jussiaea nervosa* Poir.
- L. inclinata* Gomez, l. c. is *Jussiaea inclinata* L. f.
- L. juncea* Raf. Autik. Bot. 38. 1815–1840; questionably referred to *L. virgata* Michx. in Kew Index. The small flowers suggest *L. alternifolia* L., but the description is inadequate.
- L. jussiaeoides* Michx. Fl. Bor. Am. 1: 89. 1820 is *Jussiaea decurrens* DC.
- L. lutea* Bosc ex DC. Prodr. 3: 60. 1828, pro synonym, under *L. virgata*.

- L. oocarpa* Gomez, l. c. is *Oocarpon torulosum* (Arnott) Urban.
- L. palustris* L. var. *Liebmanni* Lévl. Bull. Géogr. Bot. 22: 24. 1912; referred to synonymy under *L. palustris* var. *americana* by Fernald & Griseb., *Rhodora* 37: 176. 1935. The description sounds like their var. *nana*, over which name it would have priority, but it may even belong under *L. natans*.
- L. peduncularis* Gomez, l. c. is *Jussiaea peduncularis* Wright.
- L. pruinosa* Raf. Autik. Bot. 38. 1815-1840. "From Alleghany Mts. and Kentucky," a fact limiting the possibilities. Cannot be *L. alternifolia* L., to which referred by Index Kewensis, because of long petals and sessile leaves. I cannot place it definitely.
- Isnardia ramosior* L. ex Jackson, Index Linn. Herb. 91. 1912; nomen?
- L. ramosissima* Roth, Catalect. fasc. 3: 24. 1806; from description is in sect. *Dantia*, near *L. palustris* or *L. natans*.
- L. ramulosa* Gomez, l. c. is *Jussiaea repens* var. *peplodes* (HBK.) Griseb.
- L. rudis* Walt. Fl. Car. 89. 1788; according to Torrey & Gray, Fl. N. Am. 1: 526. 1840 there are no specimens in the Walter Herb.; I do not place it.
- L. Sagraeana* Gomez, l. c. is *Jussiaea suffruticosa* var. *ligustrifolia* (HBK.) Griseb.
- L. scabriuscula* Kell. Proc. Calif. Acad. 7: 78. 1876; is *Ammania latifolia* L. according to Kew Index.
- Isnardia subhastata* R. & P. Fl. Peruv. 1: 66. 1798; is *Ammania latifolia* according to Kew Index.
- L. Swartziana* Baill. ex Lances. Pl. Util. Colon. Franc. 457. 1866 from Martinique; unknown to me.
- L. tepicana* M. E. Jones, Contr. W. Bot. 15: 131. 1929; is *Heimia salicifolia*; cf. Standley, Field Mus. Pub. Bot. 8: 28. 1930.
- L. tuberosa* Raf. Ann. Nat. 15. 1820; *L. virgata* ? according to Kew Index, but from wrong region. I cannot place it.

POMONA COLLEGE

CLAREMONT, CALIFORNIA

DROSERA IN EASTERN NORTH AMERICA

FRANCES E. WYNNE

Confusion in the current manuals among *Drosera longifolia*, *Drosera anglica*, and *Drosera intermedia* has led to the present investigation of the eastern species of sundew. The puzzle was found to result from a nomenclatural tangle between two clear-cut species.

Linnaeus described *Drosera longifolia* in 1753 in his *Species Plantarum*. Hudson described *Drosera anglica* in 1778 in the *Flora Anglica*, and in 1800 Hayne proposed *Drosera intermedia* in Schrader's *Journal für die Botanik*.

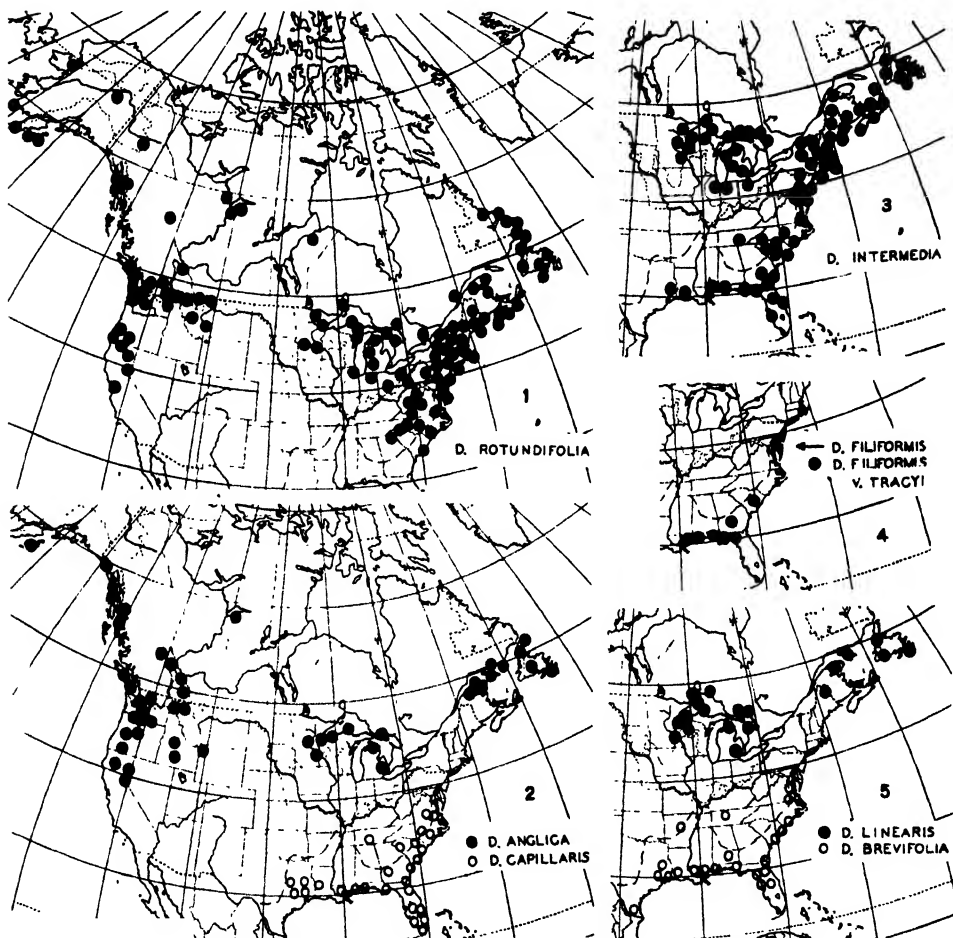
Herbarium specimens labelled *D. longifolia*, *D. anglica*, and *D. intermedia* were examined. They fall into two groups on the basis of their stipules and seeds. Group 1 is characterized by adnate stipules, and black, fusiform, striate-areolate seeds. Group 2 has free stipules and brown, oblong, papillose seeds. The leaves in group 1 tend to be elongate-spatulate, whereas those in group 2 tend to be obovate. However, some plants in each could, on the basis of their leaves, be placed in the other group, so that leaf characters alone cannot be used as a basis for specific distinctions.

The distribution of groups 1 and 2 was mapped and the ranges were found to be characteristic and distinct. Group 1 occurs in the Rocky Mountains, around the Great Lakes, and in Eastern Quebec and Newfoundland (fig. 2). Group 2 occurs along the coast of eastern North America from Newfoundland to Louisiana and around the Great Lakes (fig. 3). The ranges overlap in only two areas—the Great Lakes region and in eastern Canada.

The next problem was determining the correct names applicable to the two species. I am proposing, for the reasons discussed in the following pages, the adoption of *D. anglica* Huds. for the plants in group 1 and of *D. intermedia* Hayne for those in group 2. Linnaeus' *D. longifolia* is the oldest name and it should be used if we could determine whether it was originally applied to the plant here called *D. anglica*, or to *D. intermedia*, or to both. Neither the original description nor pre-Linnaean references mention the only satisfactory characters by which they may be separated—the stipules and the seeds. Leaf shape, which is described, cannot be used to determine what plant Linnaeus had. Furthermore, no report of an examination of Linnaeus' type is known to the author.

If we trace the interpretation of the species of *Drosera* through the literature, we find continuous nomenclatural confusion. In Hudson's treatment of *Drosera* in 1778 (*Fl. Angl.*, 135) he proposed *D. anglica* as a new species and recognized also *D. rotundifolia* and *D. longifolia*. The distinguishing characters he gives are “. . . floribus . . . hexagynis” and “. . .

capsulis trivalvis" for *D. longifolia*, and "... floribus octogynis" and "... capsulis quadrivalvis" for *D. anglica*. By 1800, however, it had been observed by Hayne that this division of the capsule into 3 or 4 (and sometimes 5) parts is not constant within a species but occurs occasionally in all the species. Early botanists, nevertheless, often gave capsule characters as the only differences between these closely related species.



FIGS. 1-5. Distribution in North America of the species of *Drosera*.

Smith in his *Flora Britannica* (1: 347. 1800) uses *D. longifolia* and *D. anglica* in the same sense as Hudson. He adds a distinction in the leaf shape: *D. longifolia* is described as "foliis obovatis" and *D. anglica* as "foliis oblongis obtusis."

Hayne in treating *Drosera* in Schrader's *Journal für die Botanik* (1800(1): 37-39. 1801) includes the species *D. rotundifolia*, *D. longifolia*,

and his new species *D. intermedia*. In the list of distinguishing features for *D. intermedia* is found: "4) *Capsula* tri—s. quadrivalvi, nec quadri—s. quinquevalvi. 5) *Seminibus* obovatis, verrucosis, *arillo* destitutis." *D. longifolia* is described in part as follows: "*Capsula* . . . quadri—s. quinquevalvis . . . *Semina* . . . *arillo* scobiformi, membranaceo, reticulatim venoso tecta." Schrader has added the following in a footnote: "Nach einem Exemplare der *D. anglica* zu schliesen, welches Herr Dr. Nohden von England mitgebracht hat, ist Herrn Hayne's *D. intermedia* die eigentliche *D. longifolia* Linn., seine *D. longifolia* aber hingegen, die Hudson'sche *D. anglica*." It is true that Hayne's *longifolia* is Hudson's *anglica*. Whether Hayne's *intermedia* is Linnaeus' *longifolia* is problematical.

Dreves & Hayne (Choix de plantes d' Europe 1: 42, 43. 1802) follow Hayne and use the names *D. intermedia* and *D. longifolia* with no mention of Hudson's *D. anglica* among the species or synonyms. *D. longifolia* is illustrated (pl. 75) with attenuate, fusiform, striate-areolate seeds whereas the seeds of *D. intermedia* are shown as blunt, obovate, and papillose.

Seeds of *Drosera* had been illustrated only once prior to 1802. Schkuhr in the *Botanisches Handbuch* (1791) illustrates and describes *D. rotundifolia* and *D. longifolia*. *D. longifolia* is shown with blunt, obovate, papillose seeds—seeds identical with those which Dreves & Hayne illustrate for *D. intermedia*. Schkuhr, however, since he does not split *D. longifolia* L., obviously had *D. intermedia* Hayne, and his treatment further confuses the interpretation of *D. longifolia* and *D. intermedia*.

De Candolle (Prodr. 1: 318. 1824) was the first to discard the name *D. longifolia* entirely and use *D. intermedia* ("seminibus exarillatis") and *D. anglica* ("seminibus arillatis"). Other authors use the name *D. longifolia* indiscriminately for first one species and then the other with either *D. anglica* or *D. intermedia* as a companion. A brief summary of the most important publications will show how the names were shuffled. Schultes in his revision of Linnaeus' *Systema vegetabilium* (6: 761. 1820) includes in his description of *D. longifolia* "Caps. 3-4—valvis. Semina obovata, glandulis elevatis obsessa, arillis destituta." Of *D. anglica* he says in part: "Caps. 4-5 valvis. Semina arillo-reticulato." Hooker (Brit. Flora. 148, 149. 1830) describes *D. longifolia* ". . . seeds with a compact rough coat not chaffy" and *D. anglica* ". . . seeds with a loose chaffy coat." The contrasting characters are given as follows: "Here [*D. anglica*] the seed . . . has a very loose, reticulated, even coat. In *D. longifolia* the coat firmly adheres to the rest of the seed, and is rough or papillose." Koch (Synopsis, 90. 1837) treats *D. anglica* as a synonym of *D. longifolia* L. and includes also *D. intermedia*. Torrey and Gray (Fl. N. Am. 1: 146. 1838) use *D. longifolia* for the plant with "seeds oblong, slightly punctate, the testa not arilliform" and *D. anglica* for the plant which has "seeds with an arilliform testa." In *Flora*

Rossica (1: 261. 1842) Ledebour includes *D. longifolia* and *D. intermedia* with *D. anglica* placed as a synonym of *D. longifolia*. He does not mention the seeds in his diagnostic characters. Grenier & Godron in *Flore de France* (192. 1847) say of *D. longifolia*: "Graines oblongues-ovoïdes, un peu rugueuses; épisperme lâche, prolongé aux deux extrémités" and of *D. intermedia*: "Graines ovales-oblongues, fortement tuberculeuse, à épisperme ou teste exactement appliqué."

Planchon, however (Ann. Sci. Nat. III. 9: 198-200. 1848), follows de Candolle, discarding *D. longifolia* L. entirely and using *D. intermedia* and *D. anglica*. Watson (Index, part 1, 353, 354. 1878), Macoun (Canadian Plants 1: 165, 166 1883), and Parlatore (Fl. Ital. 9: 212-216. 1890) do likewise.

It is apparent, then, that the literature in the century and a half following Linnaeus can be of little help in indicating which plant Linnaeus described as *D. longifolia*. It is likewise apparent that since 1800 two distinct species have been recognized. The epithet *longifolia* has been used for both these species. For the sake of argument let us call the plant with striate-areolate seeds *D. anglica* and the one with papillose seeds *D. intermedia*. Then wherever *D. longifolia* and *D. anglica* are recognized let us substitute *D. intermedia* for *D. longifolia*; where *D. longifolia* and *D. intermedia* are recognized let us substitute for *D. longifolia*, *D. anglica*. We then find the nomenclatural confusion eliminated and the concept of *D. anglica* and *D. intermedia* consistent and clear.

Current manuals remain confused in their nomenclature. *D. anglica* with adnate stipules and "loosely faveolate" [sic.] seeds and *D. longifolia* with stipules nearly free and papillose seeds are included in Gray's Manual (ed. 7, 440. 1908). Britton and Brown (Ill. Fl. 2: 203, 204. 1936) and Rydberg (Fl. Prairies and Plains, 386. 1932) use the name *D. intermedia* for the plant with papillose seeds and the name *D. longifolia* for the plant with striate-areolate seeds. Only one of these two species occurs in southern United States and *D. intermedia* has been consistently used in the manuals covering this area. The other species occurs in the west and it has been called *D. longifolia* in manuals for that area.

The preceding synopsis does not cite every publication in which *D. intermedia*, *D. longifolia*, and *D. anglica* have been used. It is sufficient, however, to indicate the continuous confusion that has existed ever since the three names appeared in the literature. Since it is impossible to determine to which species the name *D. longifolia* should be applied, it is the author's opinion that the name should be abandoned as a source of confusion until the type can be examined. An examination of the type is impossible at the present time. Article 62 of the *International Rules of Botanical Nomenclature* (ed. 3. 1935) states: "A name of a taxonomic group must be rejected if, owing to

its use with different meanings, it becomes a permanent source of confusion or error." Therefore, *D. longifolia* should be rejected and *D. anglica* and *D. intermedia* should be adopted. If, at a subsequent date, an examination of the Linnaean type of *D. longifolia* is possible, it would be necessary to substitute the name *D. longifolia* for one of the other two names. Until such time, however, the author proposes the following treatment which adopts both *D. anglica* and *D. intermedia* and rejects *D. longifolia* as a *nomen ambiguum*. This was done by several authors mentioned above and by Diels in Engler's *Das Pflanzenreich*. The author knows of only one recent treatment of North American plants which has adopted this procedure (Trans. Wis. Ac. 27: 235. 1932).

The other eastern species of *Drosera*, with the possible exception of *D. filiformis* var. *Tracyi*, present no problems. In 1914 Macfarlane proposed *D. Tracyi* as a new species. Previously, however, in 1906, Diels in *Das Pflanzenreich* published *D. filiformis* var. *Tracyi* "(Macfarlane msc. sub. titulo speciei)." Because the plant which grows along the coast from South Carolina to Mississippi differs from the one which grows on the coast from Massachusetts to Delaware only in its size and the color of pubescence, the author is following Diels and maintaining the southern variant as *D. filiformis* var. *Tracyi*. In all other characters of leaves, stipules, flowers, and seeds it is identical with the more northern *D. filiformis*.

Seven species of *Drosera* occur in eastern North America. Heretofore, no emphasis has been placed on characters presented by the seeds of sundews. In fact, they have been too briefly and inaccurately described and never adequately illustrated. This is unfortunate, for the seeds of the seven species are beautifully distinct and offer a great aid in identification. Using only leaf shape, it is not always possible to distinguish *D. intermedia* from *D. anglica*; and the leaves of certain forms of *D. capillaris* and *D. brevifolia* can be mistaken for *D. rotundifolia*. However, by means of stipules and seeds the species of *Drosera* in eastern North America are easily separated. For this reason the seeds are carefully described and illustrated here.

DROSERA L. Gen. Pl. 89. 1737; Sp. Pl. 281. 1753.

Rorella Hall, in Rupp. Fl. Jen. 114. 1745.

Esera Neck. Elem. Bot. 2: 160. 1790.

Dismophyla Raf. Fl. Tellur. 3: 36. 1836.

Adenopa Raf. Fl. Tellur. 3: 37. 1836.

Filicirna Raf. Fl. Tellur. 3: 37. 1836.

Sondera Lehm. Pugill. 8: 44. 1844.

Annual, biennial, or perennial insectivorous herbs of bogs and marshes. Leaves alternate, usually basal, tufted, covered with long glandular hairs which copiously exude a clear, viscid secretion. Blades filiform to peltate, circinate in vernation. Stipules scarious, variously fringed or divided, adnate or free (lacking in one of our species). Inflorescence a cincinnus [not

a raceme], nodding at the undeveloped apex. Flowers regular, hypogynous, generally pentamerous. Sepals 4-8 (usually 5), withering-persistent, distinct or united at the base. Petals 4-8 (usually 5), white, pink, or purple, broadened at the tip, distinct or slightly united at the base. Stamens 4-8, as many as the petals, with subulate or filiform filaments and extrorse, versatile anthers. Ovary superior, sessile, 1-celled, many-ovuled with 3-5 parietal placentae. Ovules subglobose or ovoid in 2-5 rows on each placenta. Styles 2-5, (usually 3), bipartite to the base. Capsule 2-5 (usually 3) valved. Seeds minute, anatropous, numerous, stipitate; the testa loose and variously reticulated and ornamented.

Leaf-blades filiform, not distinct from the petiole ... 1. *D. filiformis*.
 Leaf-blades expanded, distinct from petiole.

Leaf-blades suborbicular, broader than long; seeds sigmoid-fusiform, finely longitudinally striate ... 2. *D. rotundifolia*.

Leaf-blades linear, spatulate, or cuneate; seeds variously ornamented.

Stipules adnate.

Leaf-blades linear; seeds rhomboidal, crateriform, 0.5-0.8 mm.

long ... 3. *D. linearis*.

Leaf-blades elongate-spatulate; seeds fusiform, areolate-striate,

1-1.5 mm. long ... 4. *D. anglica*.

Stipules free or lacking.

Stipules conspicuous, free, scape glabrous.

Flowers white, 7-8 mm. in diameter, petals 4-5 mm. long; seeds

irregularly and densely covered with long papillae, 0.7-1.0

mm. long ... 5. *D. intermedia*.

Flowers pink, 10 mm. in diameter, petals 6-7 mm. long; seeds

papillose-corrugated with 14-16 ridges, 0.4-0.5 mm. long ... *D. capillaris*.

Stipules absent, scape glandular-pubescent, seeds crateriform, 0.3-

0.4 mm. long ... 7. *D. brevifolia*.

1. DROSERA FILIFORMIS Raf. Med. Rep. II. 5: 360. 1808; in Desv. Jour. de Bot. 1 (1808): 227. 1809.

Drosera tenuifolia Willd. Enum. 340. 1809.

Stem 1-2 cm. long. Leaves erect, basal, filiform, without distinction between blade and petiole. 8-35 cm. long, covered with long, purple or green glandular hairs. Stipules adnate, fimbriate on margins, forming matted brown wool at the base of the leaves. Scape glabrous, 6-45 cm. long, bearing 4-26 flowers. Calyx and upper part of pedicel glandular-pubescent. Flowers 1-2 cm. in diameter. Sepals oblong to elliptic, glandular-pilose, 4-7 mm. long, 2-2.5 mm. wide, united at base. Petals purple (rarely white), broadly ovate, 7-15 mm. long, 5-15 mm. wide, erose at apex. Styles 3, bi-partite to the base. Capsule obovoid, 5-6 mm. long. Seeds black, 0.5-0.8 mm. long, elliptic, abruptly caudate at both ends, coarsely crateriform, the pits in 16-20 lines. Fig. 7.

DROSERA FILIFORMIS var. *typica* Wynne, var. nov.

D. filiformis Raf. Med. Rep. II. 5: 360, as to type. 1808.

Leaves 8-25 cm. long, covered with long purple glandular hairs. Scape 6-22 cm. long, bearing 4-16 flowers. Flowers about 1 cm. in diameter; petals 7-15 mm. long, 5-8 mm. wide.

Along the coast from Massachusetts to Delaware. Fig. 4.

DROSERA FILIFORMIS var. **TRACYI** (Macfarlane) Diels in Engler, Pflanzenreich
26 (IV. 112): 92. 1906.

Drosera tracyi Macfarlane in L. H. Bailey, Stand. Cycl. Hort. 2: 1077. 1914.

Differs from var. *typica* only in its pale green pubescence, larger size, and more robust habit. Leaves 25–35 cm. long, covered with long green glandular hairs. Scape 25–45 cm. tall, bearing 14–26 flowers. Flowers 1.5–2 cm. in diameter; petals 12–15 mm. long, 15 mm. wide.

Abundant in the coastal area of the Gulf states from mid-Florida to Louisiana; also in Georgia and South Carolina. Fig. 4.

2. DROSERA ROTUNDIFOLIA L. Sp. Pl. 281. 1753.

D. septentrionalis Stokes, Bot. Mat. Med. 2: 189. 1812.

D. rotundifolia var. *comosa* Fern. Rhodora 7: 9. 1905.

Stem 1–2 cm. long bearing a rosette of leaves. Petiole 1.5–5 cm. long, flat, glandular-pilose. Leaf-blade suborbicular, 0.4–1 cm. long, broader than long and much shorter than the petiole. Stipules 4–6 mm. long, adnate, fimbriate along the upper half. Scape glabrous, 7–35 cm. long, bearing 3–15 (1–25) flowers. Flowers about 4–7 mm. in diameter. Sepals oblong, 4–5 mm. long, 1.5–2 mm. wide, obtuse, united at base. Petals white to pink, spatulate, longer than the sepals, 5–6 mm. long, 3 mm. wide. Styles 3, bipartite. Capsule 5 mm. long. Seeds light brown, 1–1.5 mm. long, sigmoid-fusiform, finely and regularly longitudinally striate, shiny with a metallic luster. Fig. 6.

Common in bogs and swamps in northern North America south to California, Montana, Illinois, Wisconsin, Ohio, South Carolina, and Georgia. Fig. 1.

3. DROSERA LINEARIS Goldie, Edinb. Phil. Jour. 6: 325. 1822.

Stem 1–2 cm. long with a rosette of erect leaves. Petiole 3–7 cm. long, glabrous, flattened. Leaves linear, 2–5 cm. long, about 2 mm. wide. Stipules 5 mm. long, adnate, fimbriate along the margins. Scape glabrous, 6–13 cm. long, bearing 1–4 flowers. Flowers about 6–8 mm. in diameter. Sepals oblong-elliptic, minutely glandular-denticulate, 4–5 mm. long, 2 mm. wide, united at base. Petals white, obovate, 6 mm. long, 3–4 mm. wide. Styles 3, bipartite to the base. Capsule 4–5 mm. long. Seeds black, 0.5–0.8 mm. long, rhomboidal, oblong-obovate, densely and irregularly crateriform. Fig. 8.

In northeastern North America extending south to Maine, Michigan, and Wisconsin. Fig. 5.

4. DROSERA ANGLICA Huds. Fl. Angl. ed. 2. 135. 1778.

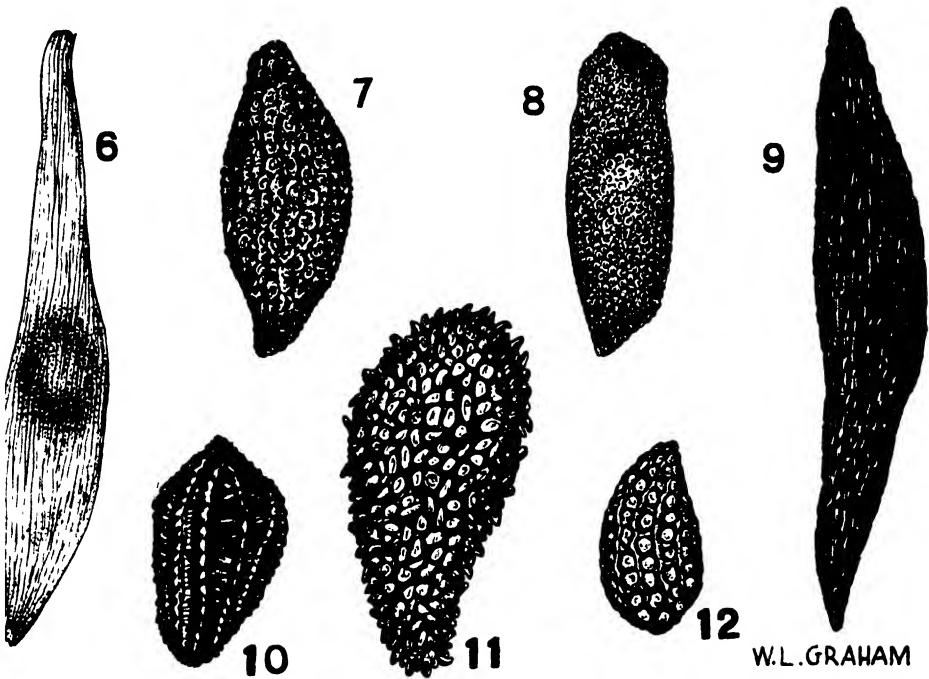
D. anglica, Gray, Man. ed. 7, 441, 1908.

D. longifolia, Britton & Brown, Ill. Fl. 2: 204. 1936; Rydberg, Fl. Prairies & Plains, 386. 1932.

Stem 1–2 cm. long bearing a rosette of leaves. Petioles 3–7 cm. long, glabrous or sparsely glandular hairy. Leaves obovate to elongate-spatulate, 3–4 mm. wide, 15–35 mm. long, with long glandular hairs on the upper surface. Stipules 5 mm. long, adnate along the entire length, fimbriate along the upper half. Scape glabrous, 6–25 cm. long, bearing 1–9 flowers. Flowers 6–7 mm. in diameter. Sepals oblong, minutely glandular-denticulate, 5–6 mm.

long, united at the base. Petals white, spatulate, 6 mm. long. Styles 3, bipartite to the base. Capsule minutely tuberculose, 4–6 mm. long. Seeds 1–1.5 mm. long, black, sigmoid-fusiform, longitudinally striate-areolate. Fig. 9.

In western North America, around the Great Lakes, and in eastern Canada. Fig. 2.



Seeds of *Drosera*. FIG. 6. *D. rotundifolia*. FIG. 7. *D. filiformis*. FIG. 8. *D. linearis*. FIG. 9. *D. anglica*. FIG. 10. *D. capillaris*. FIG. 11. *D. intermedia*. FIG. 12. *D. brevifolia*. All $\times 80$.

5. *DROSERA INTERMEDIA* Hayne in Schrad. Jour. Bot. 1800 (1): 37. 1801.

D. longifolia Michx. Fl. Bor. Am. 1: 186. 1803.

D. americana Willd. Enum. 340. 1809.

D. foliosa Elliot, Sketch 1: 376. 1817.

D. intermedia β *corymbosa* DC. Prodr. 1: 318. 1824.

D. intermedia γ *americana* DC. Prodr. 1: 318. 1824.

D. longifolia Gray, Man. ed. 7, 441. 1908.

D. intermedia Britton & Brown, Ill. Fl. 2: 203. 1936; Rydberg, Fl. Prairies and Plains, 386. 1932.

D. intermedia f. *corymbosa* Fern. Rhodora 40: 333. 1938.

Stem 1–8 cm. long, bearing leaves in a rosette and/or at intervals for several centimeters along the stem. Petioles 2–5 cm. long, glabrous. Leaves oblong spatulate to obovate, 4–5 mm. wide, 8–20 mm. long, bearing long glandular hairs on the upper surface. Stipules adnate at the base for the first millimeter, then breaking into several setaceous segments 2–5 mm. long. Scape erect, glabrous, 9–20 cm. long, bearing 9–20 flowers. Flowers 7–8 mm.

in diameter. Sepals oblong, 3–4 mm. long, 1–1.5 mm. wide, united at base. Petals white, 4–5 mm. long, 3–5 mm. wide. Styles 3 (rarely 4), bipartite. Capsule 4–5 mm. long. Seeds 0.75–0.95 mm. long, reddish brown, oblong, blunt at the ends, densely and irregularly covered with long papillae. Fig. 11.

Northeastern North America; around the Great Lakes and along the coast from Newfoundland to Texas. Fig. 3.

6. *DROSERA CAPILLARIS* Poir. *Encycl.* 6: 299. 1804.

D. brevifolia β *major* Hook. Hook. Jour. Bot. 1: 194. 1834.

D. rotundifolia var. *capillaris* Eaton & Wright, N. Am. Bot. 230. 1840.

D. minor Wood, Class-Book, 251. 1861.

Stem 1–2 cm. long, bearing a rosette of leaves. Petiole 0.6–4 cm. long, sparsely glandular-pilose. Leaves broadly spatulate, 0.5–1 cm. long, 3–5 mm. wide, usually shorter than petiole. Stipules free, or adnate for the first millimeter, then breaking into numerous setaceous segments 3–5 mm. long. Scape glabrous, 4–20 (35) cm. long, bearing 2–20 flowers. Flowers about 1 cm. in diameter. Sepals oblong-elliptic, 3–4 mm. long, 1–2 mm. wide, obtuse, united at base. Petals pink, 6–7 mm. long, 2–3 mm. wide. Styles 3, bipartite to the base. Capsule 4–5 mm. long, surpassing the calyx. Seeds brown, 0.4–0.5 mm. long, elliptic to oblong-ovate, asymmetric, coarsely papillose-corrugated in 14–16 ridges. Fig. 10.

Common in the coastal area from southern Virginia to Texas. Fig. 2.

7. *DROSERA BREVIFOLIA* Pursh, Fl. Am. Sept. 1: 211. 1814.

Stem 1–2 cm. long, bearing a rosette of leaves. Petiole 5–10 mm. long, glabrous, dilated. Leaf-blades cuneate, 4–10 mm. long, usually longer than the petiole. Stipules absent or reduced to one or two minute setaceous segments. Scape 4–9 cm. long, glandular pubescent, bearing 1–8 flowers. Flowers about 1.5 cm. in diameter. Sepals glandular-pubescent, oblong-ovate, 2.5–3.5 mm. long, 1.5–2.5 mm. wide. Petals rose to white, obovate, 4–5 mm. long, 2–3 mm. wide. Styles 3, bipartite to the base. Capsule 3 mm. long. Seeds black, 0.3–0.4 mm. long, obovate, oblong, caudate at base, crateriform, the pits in 10–12 rows. Fig. 12.

In the coastal area, where it is common, from southern Virginia to Texas, Florida, and Missouri. Fig. 5.

EXCLUDED NAME

Drosera longifolia L. Sp. Pl. 281. 1753. *Nomen ambiguum.*

THE NEW YORK BOTANICAL GARDEN
NEW YORK

**A DISCUSSION OF THE OCHNACEOUS GENUS FLEURYDORA
A. CHEV. AND THE ALLIED GENERA OF THE
LUXEMBURGIEAE**

JOHN D. DWYER

In 1933 Auguste Chevalier (1) described the genus *Fleurydora* from material collected near Kinda, French Guinea. A study of his description and plate (cf. his figure 1, 1-9) convinced me that Chevalier erred in placing the new genus in the tribe Euthemidae Planchon; this previously consisted of the single genus *Euthemis* Jacq. with six species described from Borneo and Sumatra. Hutchinson (2) recently brought this error to light and reclassified *Fleurydora*, relating it to two American genera of the Ochnaceae, *Blastemanthus* Planchon and *Godoya* R. and P. Unfortunately he resurrected van Tieghem's tribe Blastemantheae, described in 1904, and placed the trio of genera therein. Apparently on the grounds that van Tieghem's treatment of the Ochnaceae is a "celebrated classification," Hutchinson elected to rely on his work to a marked extent. He proceeded in turn to criticize Chevalier's classification without himself manifesting a clear understanding of the complex tribe Luxemburgieae from which he separated the Blastemantheae.

I have spent more than two years in studying the American genera of the Luxemburgieae and feel qualified to discuss relationships within this tribe. Hutchinson's initial error lies in accepting van Tieghem's work without critical analysis. He admits that van Tieghem based his classification "mainly on anatomical characters." Several workers¹ attest to the unsoundness of van Tieghem's study of the Ochnaceae (3), indicating that his criteria of classification are unorthodox, viz., his splitting of the genus *Ouratea* into thirty-four genera and his many new species described without adequate morphological descriptions and accompanying keys.

Fleurydora A. Chev. is obviously not related to the genus *Euthemis* Jacq., since as Hutchinson himself points out, "the tribe Euthemidae is characterized especially by the possession of only *two ovules* in each loculus of the ovary, and in having a baccate fruit composed of five pyrenes." He then reclassifies *Fleurydora*, placing it in the Blastemantheae and indicating the affinity of this tribe with the Luxemburgieae on the basis of its numerous ovules and capsular fruit. Preceding the formal description of his revised

¹ Beauverd, G (Le genre *Luxemburgia*. Bull. Soc. Bot. Genève II. 7: 232. 1916.) states: "... au sens de van Tieghem ... la notion du tribu ... s'applique exactement à notre conception du genre. ..." Riley, A. M. (Mexican and Central American Species of *Ouratea*. Kew Bull. 1924: 102. 1924) points out at some length the weaknesses of van Tieghem's work.

tribe Blastemantheae, Hutchinson asserts that the "character of the very unequal-sized and spirally arranged sepals is shared only by these three genera of the Ochnaceae," *Blastemanthus*, *Godoya*, and *Fleurydora*, the three genera of his emended tribe. This statement does not agree with the facts, since *Rhytidanthera* van Tieghem, *Krukoviella* A. C. Smith, and *Poecilandra* Tulasne, three American genera of the Luxemburgieae, have unequal sepals similarly arranged. In fact the sepals of *Rhytidanthera*, the only pinnately-leafed genus of the Ochnaceae, are the prototypes of those of *Godoya* in every detail. This character, as well as less obvious characters, demonstrate the close relationship existing between *Godoya* and *Rhytidanthera*. Both of these are closely allied with the genus *Cespedezia* Goudot principally on the basis of the following characters: the fimbriate appendages (glands?) located at the proximal and inner surface of the bracts and sepals, the coriaceous and estylate and pentacarpellate pistil with intrusive T-shaped parietal placentae and with sessile radiating stigmas, and lastly the distinctly alate seeds. *Krukoviella* agrees with the above genera in all these characters except that the sepals lack appendages. Its close relationship with *Godoya* is manifested in the shape, texture, and venation of the leaf-blades, in the texture and shape of the sepals (here often subequal in length), and in the dehiscence of the anthers by a single instead of two terminal pores. The genus *Blastemanthus*, in turn, gives evidence of its relationship with *Godoya*, *Rhytidanthera*, *Cespedezia*, and *Krukoviella* in the texture and shape of the sepals, anthers, and pistil, the eccentric position of the pistil at anthesis, and the intrusive T-shaped parietal placentae bearing numerous imbricate ovules. The presence of subulate staminodia links *Blastemanthus* to the remaining American genera of the tribe. While several species of *Poecilandra* have some of their staminodia the prototypes of *Blastemanthus*, the relationship existing between these genera is evident, especially in their vegetative characters. *Blastemanthus* is more closely related to a recently described ochnaceous genus, *Tyleria* Gleason, since it possesses alate seeds and terminally poricidal and unequal-celled anthers as well as a subulate style. *Tyleria* is closely related to the three remaining American genera of the Luxemburgieae, all of which are herbaceous.

Hutchinson in his discussion of *Fleurydora* omits much of importance. In the first place he circumvents van Tieghem's tribe Godoyeae and shifts without explanation the type genus of the Godoyeae to the closely related tribe, Blastemantheae. In his description of the latter tribe he states simply that the fruit is a capsule. One of the striking characters of the genus *Blastemanthus*, a character which Hutchinson does not describe or discuss, and which in my opinion demands consideration, is the *reduction* in seed number to one or two per carpel; this condition is correlated with an infolding in the fruit of one or of both of the margins of each of the three carpels,

one of the paired margins being non-seminiferous (see figure 1, *h*) ; the seeds of *Blastemanthus* are exceptionally large and are nonalate (fig. 1, *j*). Thus in the character of its fruit *Blastemanthus* differs from *Godoya* and *Fleurydora*, as well as from the remaining American genera of the Luxemburgieae. In my opinion the internal structure of the fruit of *Blastemanthus* provides some evidence for upholding a distinct monogeneric tribe Blastemantheae. However I am retaining it in the tribe Luxemburgieae in light of the other characters discussed above.

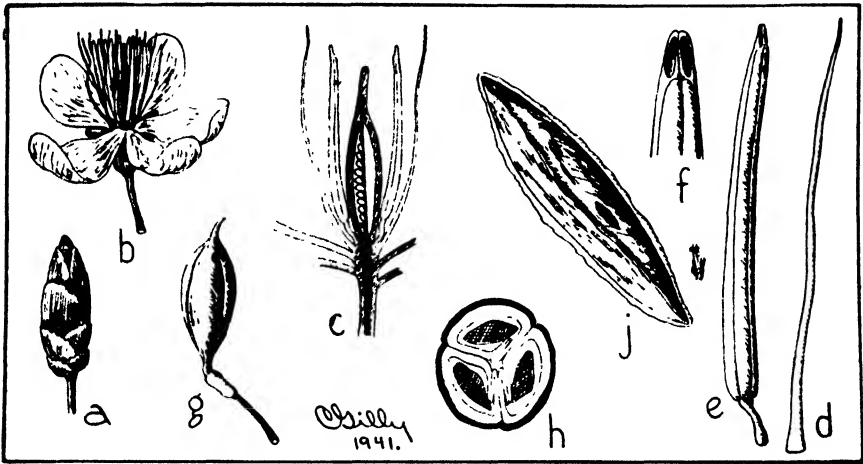


FIG. 1. *Blastemanthus grandiflorus* Spruce: a—bud ($\times 1$); b—flower ($\times 1$); c—longitudinal section through flower ($\times 2$); d—coronal segment ($\times 4$); e—stamen ($\times 4$); f—apical portion of anther, ventral view, showing dehiscence pores ($\times 8$). (a, drawn from Spruce 2012; b-f, drawn from Ducke 297.) *B. gemmiflorus* (Mart. and Zucc.) Planch.: g—capsule ($\times 1$); h—cross-section of mature capsule, showing placentation ($\times 2$); i—longitudinal section of capsule ($\times 2$); j—seed ($\times 5$). (g-j, drawn from Spruce 3709.)

To establish the relationship between *Fleurydora* and the genera of the Luxemburgieae is difficult. Several lines of evidence indicate that the New World genus *Pocilandra* is closely allied with Chevalier's genus; the leaf-blades are similar in shape, retuse at the apex, and have closely crowded secondary veins; the sepals are similarly disposed and comparable in texture, while the style is subulate, and the seeds are short-alate, although the wing in *Pocilandra* is about equal at each end of the oblong body of the seed. One important character, however, demonstrates that *Fleurydora* is related at least in part to the *Godoya*, *Rhytidanthera*, *Krukoviella*, *Cespedezia*, and *Luxemburgia* complex: the pattern of the placentation. Many workers (including Chevalier in his work on *Fleurydora*) state that the placentation is axial and hence the ovary is 3-5-loculate depending upon the number of carpels characterizing the particular genus. My observations show that the genera listed above have intrusive parietal placentation and that the

ovary is *uniloculate*. Although material of *Fleurydora* is not available for dissection, I anticipate that Chevalier in his figure of the cross-section of the ovary (see his figure 1, no. 9) has erred on the matter of placentation, as many authors have done in describing and figuring the ovaries of the genera of the above complex. I have found that the adjacent margins of the carpels pass into the locule in a paired condition and as they approach the axial "line" bifurcate, with each margin curving; a cross-section shows 3-5 T-shaped parietal placentae with the minute imbricate ovules borne on the abaxial face of each end of the T. Undoubtedly the thick-walled ovary, crassate placentae, and the abundance of ovules have caused workers to err in their description of the placentation.

SUMMARY

We may therefore conclude that Chevalier's genus *Fleurydora* belongs to the tribe Luxemburgieae and that it is related to several of the American genera of the tribe, particularly to *Pocilandra*. The tribe Luxemburgieae, as far as the American genera are concerned, is more comprehensive than maintained by either van Tieghem or Hutchinson.

The author wishes to thank Mr. Charles Gilly of the New York Botanical Garden who supplied the figure of *Blastemanthus*.

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ANOTHER NEW NAME IN VACCINIUM

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For a number of years it was customary to refer to the North American lowbush material of *Vaccinium* subgenus *Cyanococcus* having shining green leaves with sharply serrate margins and blue fruit as *Vaccinium pensylvanicum*. Later, it was pointed out that *V. pensylvanicum* Miller (Gard. Diet. ed. 8. 1768) referred to a non-vacciniaceous plant. The next oldest valid name for any part of this material was *Vaccinium angustifolium* Aiton (Hort. Kew. ed. 1. 2: 11. 1789).

More recently Longley (Science **66**: 566-568. 1927) reported that *Vaccinium angustifolium* was tetraploid. Work now in progress indicates that "*V. angustifolium*" consists of two rather distinct entities, one diploid ($n = 12$), the other tetraploid ($n = 24$), which seem incapable of producing fertile hybrids. Therefore, such plants as might appear to be connecting intergrades are not the result of hybridization between these two followed by segregation, but the result of differential responses to environmental conditions. Where they grow together under the same conditions, the tetraploid is easily distinguished from the diploid by its greater height, coarser branching habit, larger flowers and leaves (the leaves are usually a deeper green), and much larger fruit. These differences seem to be the standard result of the advent of polyploidy in *Vaccinium*.

All of the available evidence points to the fact that the nomenclatural type of *V. angustifolium* Ait. belongs to the diploid population. It is therefore thought that some name should be found which might be applied to the tetraploid population. In searching through the literature, we find that Lamarck has given us an excellent description of this coarser plant, outlining in considerable detail the characters such as height of plant, size of leaf, flower, and fruit, which we now know serve to distinguish the tetraploid from the diploid, even noting that the plant came from Pennsylvania, where the tetraploid is relatively abundant.¹ Unfortunately, Lamarck applied the name *V. pensylvanicum* to his plant. In supplying a name for this tetraploid population, the following has been chosen:

¹ It is quite likely that the material sent to the Jardin du Roi—and from which Lamarck drew his description—was selected for size of berry, a natural thing to do. Several years ago I examined a plot containing more than a hundred of the late F. V. Coville's selections of "*V. angustifolium*." These selections were made primarily on the basis of the size of berry. So far, each of these examined has proved to be tetraploid; and it was from this group of plants that the material studied by Longley was obtained.

Vaccinium lamarckii, Camp, nom. nov. *Vaccinium pensilvanicum* Lam. Encyc. 1: 74. 1783. Not *Vaccinium pensilvanicum* Miller, Gard. Diet. ed. 8. 1768.

There is, of course, the problem of status. On the basis of the general morphological affinities, it might seem advisable to treat *V. lamarckii* as a genetic subspecies of *V. angustifolium*; but to do so might be laying the way open for a future cumbersome nomenclatural situation. For example: being tetraploid, the relatively lowbush *V. lamarckii* hybridizes freely with the highbush *V. corymbosum* in certain areas; in fact, as will be pointed out in later papers, it is the source of certain of the notable variant forms of *V. corymbosum*. On the other hand, genetically, it is completely disjunct from the diploid *V. angustifolium*. Actually, the apparent intergrades between *V. angustifolium* and *V. lamarckii*, the result of plants of both growing under unusual environmental conditions, are no greater in number and no more troublesome of identification than the "lamarckoid" segregates of *V. lamarckii* \times *V. corymbosum*; yet we would not think of combining these latter two entities under the same binomial. It is therefore thought best to treat *V. angustifolium* and *V. lamarckii* as separate species, at least in the preliminary stages of our investigation. It has the further advantage, for the present, of clarifying the nomenclatural and phyletic situation in a group which contains differentiated and genetically disjunct pairs of diploids and derived tetraploids, such as: *V. caesariense* and *V. australe*; *V. atrococcum* and *V. arkansanum*; *V. pallidum* and *V. simulatum*; *V. tenellum* and *V. virgatum*; *V. torreyanum* ("vacillans") and *V. tallapusae*; as well as *V. angustifolium* and *V. lamarckii*.

THE NEW YORK BOTANICAL GARDEN
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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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C. STUART GAGER

December 23, 1872—August 9, 1943

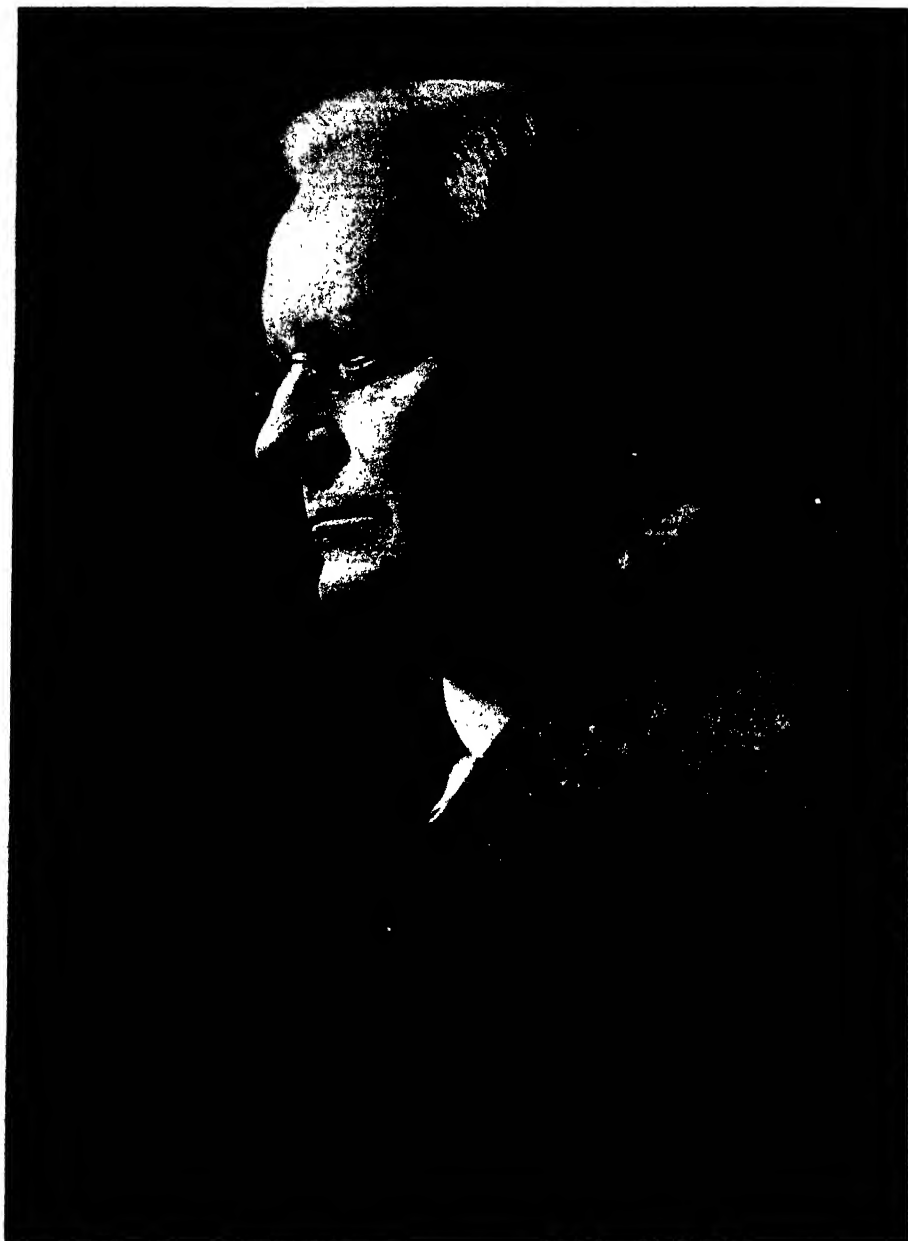
GEORGE M. REED AND ARTHUR H. GRAVES¹

Charles Stuart Gager, the son of Charles Carroll and Leora Josephine (Darke) Gager, was born at Norwich, N. Y., where he spent his boyhood and obtained his elementary education in the local public schools. In the fall of 1891 he attended Syracuse University, graduating with the A.B. degree in 1895. During his senior year he served as undergraduate laboratory assistant in the Department of Biology, which was in charge of Dr. Charles W. Hargitt.

Following his graduation from Syracuse University, Dr. Gager was for one year (1895-1896) Vice Principal of the Ives Seminary, Antwerp, N. Y. The next year (1896-1897) he attended the New York State Normal College, Albany, N. Y., and obtained the two degrees, Bachelor and Master of Pedagogy. In the fall of 1897 he became Professor of Biological Sciences and Physiography at this institution, holding the position until September, 1904. During this period, however, he attended the Harvard Summer School in 1898, served as Assistant in Botany at Cornell University (1901-1902), and Instructor in Botany during the summer of 1904. He was Laboratory Assistant at the New York Botanical Garden (1904-1905), and in the spring of 1905 he was Acting Professor of Botany at Rutgers College, N. J. In the fall of 1905 he was teacher of Botany in the Morris High School, N. Y. He also taught Botany in the summer sessions of New York University in 1905 and 1906. He obtained his degree of Doctor of Philosophy at Cornell University in 1902, carrying on his research under the direction of Professor George F. Atkinson, his doctoral thesis being concerned with "The Development of the Pollinium and Sperm-Cells in *Asclepias Cornuti* Decaisne."

On February 1, 1906, Dr. Gager became Director of the Laboratories at the New York Botanical Garden, succeeding Dr. Daniel Trembly MacDougal, and holding this position until August, 1908. While at the Garden he devoted himself largely to research, making a special study of the effects of the rays of radium on plants. The results of his investigations were published in 1908 as a Memoir of the New York Botanical Garden. His interest in this subject continued throughout his life. He cooperated in 1927 with Dr. A. F. Blakeslee on the use of rays of radium for inducing chromosome and gene mutations in *Datura*. As recently as 1936 he prepared a chapter, "The Effects

¹ The portrait of Dr. Gager is published at the expense of the Lucien M. Underwood Memorial Fund.



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CHARLES STUART GAGER

of Radium Rays on Plants, A Brief Résumé of the More Important Papers from 1901 to 1932," which was published in *Biological Effects of Radiation*, edited by Professor B. M. Duggar. Also, while he was at the New York Botanical Garden he was occupied with his translation of DeVries' work on *Intracellular Pangenesis*, which he published in 1910.

Beginning in September, 1908, for two years Dr. Gager was Professor of Botany at the University of Missouri, serving as Administrative Chairman of the department. He was in charge of the general course in botany, also teaching advanced courses in physiology and morphology. A large number of students registered for the general course at the University, mostly freshmen or sophomores in the College of Agriculture or the College of Arts and Sciences. His teaching experience during these two years led him to the preparation of his text book *The Fundamentals of Botany*, published in 1916. Accompanying this text *A Laboratory Outline in General Botany* was published, the first edition appearing in 1916, the second in 1919, and the third in 1926. He further contributed to botanical text books by publishing, in 1926, his *General Botany with Special Reference to Its Economic Aspects*.

On the first of July, 1910, Dr. Gager took up the work as Director of the newly established Brooklyn Botanic Garden, and for more than thirty-three years guided its destinies. During the earlier years he was closely associated with Mr. Alfred T. White, who is recognized as the "Father" of the Garden, and was the chief inspiration and support in the founding and early development.

Dr. Gager thought of a botanic garden as something quite different from the traditional type. His motto for the Brooklyn Botanic Garden was "For the Service of the City and the Advancement of Botany," and to him this ideal meant beautiful grounds with displays of both botanical and popular value and interest, botanical research, and public education, all of which are reflected in the history and development of the Brooklyn Botanic Garden. He laid particular emphasis upon the possibilities of botanical education as an important part of a botanic garden's activities. This led to the establishment of the curatorship of Public Instruction in 1912, and in 1913 an instructorship in this department with special supervision of the educational work for children, this phase being separated in 1916 as the Department of Elementary Instruction. The educational work with children is one of the outstanding features of the Garden's activities, for which it is widely and favorably known.

Further, Dr. Gager thought of a botanic garden as an outdoor museum of living plants. He strongly emphasized not only the botanical aspects, but the horticultural as well, stressing the value of building up horticultural collections. Thus, in the course of time, special features—*Gardens Within a Garden*—were developed. One of the earliest was the establishment of the

Local Flora, an area set aside for growing native plants that are found within one hundred miles of New York City. The *Japanese Landscape Garden* was first opened to the public on June 5, 1915, and the *Rock Garden* in the spring of 1917. The *Children's Gardens*, together with the *Children's House* were completed for use in 1916. The *Rose Garden* was opened to the public in 1927, and the *Herb Garden* and *Medicinal Plant Garden* were established in 1938.

When Dr. Gager first came to Brooklyn he had a small office space in the Academy of Music and, later, in the Brooklyn Museum building. In the fall of 1913 the first section of the *Laboratory Building*, consisting of only a small portion of the south end of the present structure, together with the adjacent conservatories, was completed for occupancy by the staff. It was not until the spring of 1917 that the rest of the building was completed, being formally dedicated on April 19-21, the ceremonies being attended by many eminent botanists, who presented formal papers on the occasion.

Dr. Gager displayed a broad interest in botanical and horticultural affairs and was an active member of many societies. He was a member of the Botanical Society of America (President, 1936), The Torrey Botanical Club (Secretary 1905-1908, Vice President, 1917-1931, President 1942), the New York Academy of Sciences (Corresponding Secretary 1941), the Society of Experimental Biology and Medicine, American Society of Naturalists, American Society of Biological Chemists, Ecological Society of America, the Genetics Society of America, Fellow of the A.A.A.S. (Vice President and Chairman of Section G in 1917), the Horticultural Society of New York (served on the Board of Directors since 1928, and Vice Chairman since 1937). He was made an honorary life member of the Pennsylvania Horticultural Society in 1934, the School Garden Association of America, the Royal New Zealand Institute of Horticulture (1940), and the Royal Agricultural and Horticultural Society of India (1941). He was a member of Phi Beta Kappa and Sigma Xi. Among special honors that Dr. Gager received was the Arthur Hoyt Scott gold medal and cash award for outstanding achievement in the field of horticulture in 1941. In 1920 Syracuse University conferred on him the honorary degree of Doctor of Science, and in 1921 the New York State College for Teachers, the degree of Doctor of Pedagogy.

Dr. Gager served on many important committees, dealing more particularly with horticultural affairs. Among others, the Committee on Plant Quarantines and their Administration, the Committee on Botanical Exhibits for the World's Fair at Chicago in 1933, Sub-committee on Scope and Function of the Planning Committee on U. S. Botanic Gardens, Washington, D. C. (1934-1936), and the Committee of the International Flower Show (1932-). He also served on the New Jersey Federation of Shade Tree Com-

missions (1934-), and the Board of Directors, American Association of Botanical Gardens and Arboretums (1940-).

His diversified interests were evidenced by his activities on the Brooklyn Civic Council, the Park Association of New York City, and the National Institute of Social Sciences, of which he was Vice President (1928-1931), President (1932-1935), and again Vice President (1935-). He was an active member and Ruling Elder of the Reformed Protestant Dutch Church of Flatbush. He was a member of the Century Association, Twentieth Century Club (President 1933-1935), the Winter's Night Club, and the Rembrandt Club.

He took an active part in the founding and carrying on of botanical journals for the publication of scientific results. He was the first Business Manager of the *American Journal of Botany*, founded in 1914, continuing until 1935, during which time twenty-two volumes were published. He also served as Business Manager for *Ecology* from its founding in 1920, and for *Genetics* since 1922.

In 1910, soon after coming to the Garden, Dr. Gager accompanied Dr. and Mrs. N. L. Britton on a trip to Cuba. In 1927 he was in Europe for several months, visiting particularly France and Italy. This visit was primarily for the purpose of gathering data on the European Botanic Gardens, since he was then engaged in the preparation of *The Botanic Gardens of the World*, the first edition of this work being published in 1937 and the second in 1938. In 1930 he attended the Fifth International Botanical Congress in Cambridge, England, again visiting botanical gardens in several European countries.

On June 25, 1902, Dr. Gager married Bertha Woodward Bagg of Rensselaer, N. Y., who was of invaluable assistance to him throughout his career because of her tact, charm, and wise counsel. They had two children, Benjamin Stuart, who was born on January 10, 1904, and died March 31, 1918, and Prudence, now Mrs. Kenneth G. Bucklin.

Dr. Gager was much sought after as a speaker for popular addresses on botanical or horticultural subjects. He had a very attractive personality, a pleasing manner in his addresses, and always gave a clear and interesting presentation of his subject.

A selected list of the writings of C. Stuart Gager

In addition to many reviews and papers chiefly on matters of horticultural and pedagogical interest, Dr. Gager, as editor of the Brooklyn Botanic Garden Record, wrote many short articles about matters relating to the Brooklyn Botanic Garden, and, each year, an extensive report of the activities of the Garden. A list of these published writings would contain more than 300 titles. We have, therefore, gathered together and arranged in chronological order the following selected list of those papers which we believe are of special importance for botanical science.

- The development of the pollinium and sperm-cells in *Asclepias Cornuti* Decaisne. A thesis submitted to the university faculty of Cornell University for the degree of Doctor of Philosophy, June, 1902. (Also Ann. Bot. 16: 123-148. 7 pl. Mr 1902.)
- Preliminary notes on the effects of radium rays on plants. (Soc. for experimental biol. and medicine. Proceedings reported by the Secretary, W. J. Gies. May 24, 1905, p. 14.) Also Am. Medicine 9²⁵: 1030. 1905.
- Tuber-formation in *Solanum tuberosum* in daylight. Torreyia 6: 181-186. S 1906.
- Further note on the formation of aërial tubers in *Solanum*. Torreyia 6: 211, 212. 25 O 1906.
- The breathing of plants. Jour. N. Y. Bot. Gard. 8: 143-156. J1 1907.
- Radium in biological research. Science 25: 589-590. 12 Ap 1907.
- Effects of the rays of radium on plants. Mem. N. Y. Bot. Gard. 4. 278 p. 14 pl. 1908.
- Some physiological effects of radium rays. Am. Nat. 42: 761-778. 17 f. 1908.
- The influence of radium rays on a few life processes of plants. (Contr. Dept. Bot. Univ. Missouri no. 16.) Pop. Sci. Mo. 74: 222-232. 1909.
- A laboratory outline for general botany. 90 p. Columbia, Mo. 1909.
- Radium rays and plant life processes. Sci. Am. Suppl. 57¹⁷³⁸: 264-265. 13 f. 1909.
- Vrie, Hugo de. Intracellular pangensis including a paper on fertilization and hybridization. Transl. from the German by C. Stuart Gager. 270 p. Open Court Publ. Co., Chicago. O 1910.
- The Brooklyn Botanic Garden. Jour. N. Y. Bot. Gard. 11: 190-191. Au 1910.
- The educational work of botanic gardens. Cyclopedia of Education. pp. 421-425. The MacMillan Co., New York. 1911. Also in Jour. N. Y. Bot. Gard. 12: 73-85. 1911. Reissued separately as Brooklyn Bot. Gard. Contr. no. 1.
- The purpose of an introductory course in botany. Proc. 24th Ann. Convention Assoc. Coll. & Prep. Schools of Middle States & Maryland. 1910: 58-65, 1911. Reissued as Brooklyn Bot. Gard. Contr. no. 2.
- Cryptomerie inheritance in *Onagra*. Bull. Torrey Club 38: 461-471. pl. 20, 21. O 1911. Reissued as Brooklyn Bot. Gard. Contr. no. 3.
- The Brooklyn Botanic Garden. Pop. Sci. Mo. 80: 338-345. Ap 1912.
- The first botanic garden on Long Island. Brooklyn Bot. Gard. Record 1: 97-99. O 1912.
- Ingrowing sprouts of *Solanum tuberosum*. Bot. Gaz. 54: 515-524. D 1912. Reissued as Brooklyn Bot. Gard. Contr. no. 5.
- The opening of buds. Brooklyn Bot. Gard. Leaflet 12: Ap 1913.
- The pollination of pines. Brooklyn Bot. Gard. Leaflet 13: My 1913.
- Botanic Garden. In: L. H. Bailey, The Standard Cyclopedia of Horticulture 1: 526-532. 1914.
- The translocation of material in dying leaves. Science 41: 99-104. 15 Ja 1915.
- Present status of the problem of the effect of radium rays on plant life. Mem. N. Y. Bot. Gard. 6: 153-160. 31 Au 1916.
- Fundamentals of botany. xx + 640 p. 434 f. P. Blakiston's Son & Co., Philadelphia. 1916.
- A laboratory guide for general botany. viii + 191 p. P. Blakiston's Son & Co., Philadelphia. 17 N 1916.
- Ideals and opportunities for a botanic garden. Brooklyn Bot. Gard. Record 6: 121-130. J1 1917.
- Forest problems of the Ashokan watershed. Brooklyn Bot. Gard. Leaflet 5¹²⁻¹³: 10 O 1917.
- The near future of botany in America. Science 47: 101-115. 1 Fe 1918.
- A brief history of the botanic garden idea in Brooklyn. Brooklyn Bot. Gard. Record 7: 99-112. O 1918.

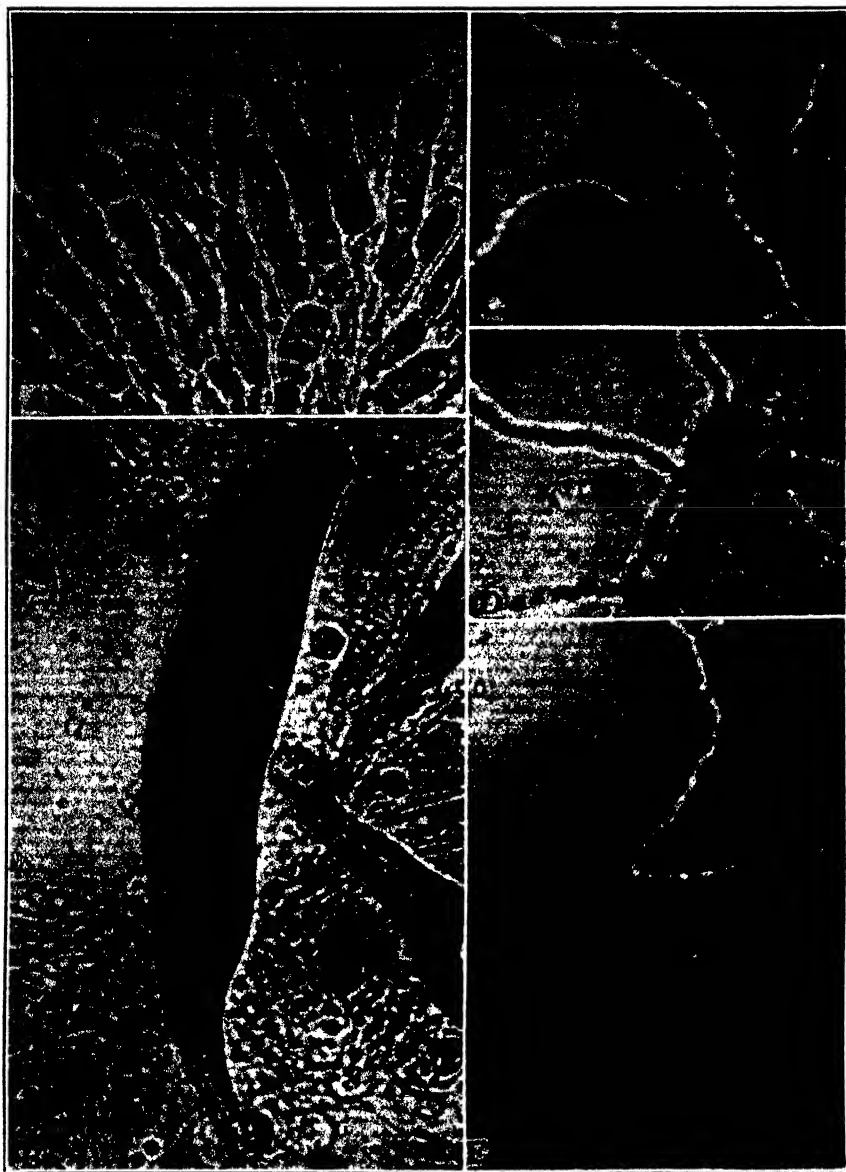


FIG. 1. A, deliquescent ascus abortion of *Neurospora tetrasperma*. All asci were homozygous, *dd*. B, indurated aborted ascus. An effect induced by cultural conditions, and not heritable as such. More highly magnified, C, germination of an abnormal ascospore of the kind rarely developed in asci homozygous for *dd*. Germination here is from a point beneath the spore. D, Growth from or "germination" of an indurated aborted ascus. Note the spherical enlargements from which secondary growth has proceeded. Such enlargements are always present when ascospores germinate. E, same as D except for the location of one of the points from which growth has proceeded. In neither case is there germination by way of the ring-pore at the ascus tip.

quently abort without spore formation.³ In this case there is a fourth nuclear division which follows very quickly the third division and this upsets the normal course of events so that no spores whatever are formed in such asci (fig. 1, B). These asci with 16 nuclei very often become heavily indurated and take on markings characteristic of the ascospores themselves. In the paper referred to it was indicated that indurated ascus abortion may be due either to heritable genetic factors or to certain cultural environmental conditions. In either case the aborted asci have the same appearance and nuclear behavior is much the same, that is, a fourth nuclear division occurs immediately following the third.

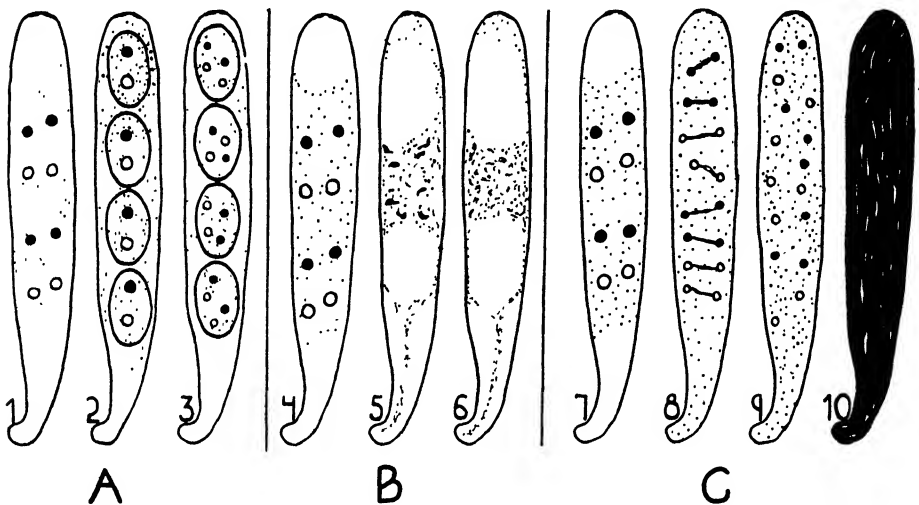


FIG. 2. Diagrams showing nuclear behavior in three types of asci of *Neurospora tetrasperma*. The reduction divisions and the third division which is always equational are not figured. In this respect the picture is the same for all three types. A, in a normal ascus four spores are delimited after the third division, two nuclei of opposite sex being included in each spore. As soon as the spores are fully delimited a fourth division occurs so that there are then sixteen nuclei present in the spore complement of each ascus. B, deliquescent ascus abortion. The eight nuclei move toward the center of the ascus and begin to degenerate. In No. 6 nuclear degeneration is complete. C, indurated ascus abortion. A fourth nuclear division follows very quickly the third division, not allowing time for spore formation. Such asci often become heavily indurated, as shown at C 10 and in Figure 1, B.

Dodge and Seaver⁴ described an interesting case where homozygous asci (*dd*), which would ordinarily abort and deliquesce, under certain cultural conditions all became indurated. In other matings many heterozygous asci

³ Dodge, B. O. A lethal for ascus abortion in *Neurospora*. *Mycologia* 26: 360-376, 1934.

⁴ Dodge, B. O. & Seaver, Bernice. The combined effects of the dominant and the recessive lethals for ascus abortion in *Neurospora*. *Am. Jour. Bot.* 25: 156-166, 1938.

(*Dd*) for the most part became indurated, while others did delimit some ascospores. Later some of the indurated asci were placed on the surface of agar in Petri dishes under conditions suitable for growth. It was found that hyphal growth seemed to occur from the under side of a few asci, but no growth could be seen from the pore located at the tip end of such as ascus. It was not possible to determine whether or not this growth may have proceeded from conidia which may have been accidentally carried over when the asci were isolated. On other occasions the same experiment was performed with the same results; no positive proof, however, that the indurated ascus actually "germinated" was obtained.

In our recent experiments on heterocaryotic vigor it was very difficult to determine positively whether or not a general heterocaryotic condition had been obtained when certain races were grown together in mixed culture. It was believed that such mixed cultures might produce some ascocarps, even though no general heterocaryotic condition had been reached through anastomoses followed by nuclear migrations. Fertilization could well occur through conidiation or spermatization. In these breeding experiments in which each of the two races mated carried the recessive lethal *d*, it was found that if the culture medium was a certain potato dextrose, homozygous asci (*dd*) not only aborted, but also frequently became indurated. Having in mind the previous experiments in which such asci gave indications of germinating, we carried out carefully controlled experiments for proving definitely that such indurated asci could be made to germinate. We are using this term "germinate" perhaps in a rather strained sense, since the term has usually been applied, in discussing the fungi, to spores which are sending out germ-tubes. We say sclerotia and bulbils germinate, however. Indurated asci are certainly not spores, even though they may have a striately marked wall like that of ascospores.

By growing our races *Ad* and *ad*⁵ together on a potato dextrose agar we were able to prevent, in certain cultures, the degeneration of the eight nuclei

⁵ *A* and *a* are the sex reaction factors, both of which must be present before an ascus will form. In addition to the recessive, *d*, there will naturally be other factors present; some will be brought along in one race, while the second race in the mating will carry the same or other factors or their alleles. There would be little point in breeding two races which differ only in their sex reaction factors. In the breeding experiments under discussion the fusion nucleus will be homozygous for some factors and heterozygous for others, but we are here concerned with only *A*, *a*, and *d*, factors for sex reaction and factors for homozygous ascus abortion, ignoring for the present the factors involved in heterocaryotic effects. We also assume here that there are 16 nuclei present in an indurated aborted ascus. Sixteen nuclei would result from four divisions, but some of these nuclei may degenerate; or there may be a fifth division, but it would be necessary to have cytological evidence for this statement. Normally, regardless of whether we have an eight-spored ascus like those of *N. crassa*, or a four-spored ascus like those of *N. tetrasperma*, there are in all the spores taken together, 16 nuclei. It is only in the early stages of spore germination that additional nuclear divisions occur.

in some asci, so that a fourth division must have occurred. We assume this is what happened because the aborted asci became indurated. In such asci the 16 nuclei do not degenerate, at least not for some time.

A number of these indurated asci were carefully isolated and placed on the surface of water agar in plates. They were then heated to 58–60° C for one hour. This treatment will kill all conidia which are in contact with a moist surface. It was found that in no case were conidia which survived the heating carried over in the process of isolating the asci. Therefore, whenever hyphal branches appeared to be emerging from beneath or from the side of an indurated ascus we were certain that it was the ascus, not contaminating conidia, that was the source of the growth. There is usually a vesicle or spherical enlargement of the germ tube from which secondary tubes proceed in two or three directions before they branch (fig. 1, D, E). If an indurated ascus can really germinate we should naturally expect the germ-tube to proceed from the pore at the ascus tip.

We do not know the exact cultural conditions which may lead to an indurated ascus abortion which is not heritable. Zickler⁶ found that by treating the cultures with chloral hydrate he could induce the formation of giant ascospores which would nevertheless germinate. He figures what he also calls giant spores which completely fill the ascus. These are certainly not spores; they are indurated aborted asci. He does not mention that he obtained out-growths from such asci. When an ascus contains only a single giant spore, the spore does not completely fill the ascus; there is always some epiplasm left outside the spore. Dodge, in his plate 3, figs. B and F,⁷ illustrates very clearly the difference between an ascus with one giant spore, and an indurated ascus.

On the other hand, there are some facts which support the view that an indurated ascus is nothing more than a giant ascospore. (1) The wall of such an ascus is beautifully striated, like that of an ascospore of *Neurospora*. (2) There is a definite ring-pore at the upper end of the ascus. Ascospores have definite germ pores at either end. (3) When an ascus germinates there develops the very characteristic spherical enlargement of the germ-tube soon after it emerges. Such vesicles do not occur when a conidium germinates or when a hyphal cell or fragment sprouts out; they are formed only when ascospores germinate. (4) Heat treatment stimulates indurated ascus germination the same as it does ascospores.

In addition to the reasons given previously in favor of the view that the ascus is a definite morphological unit regardless of how it may function abnormally, it may be said that the striations on ascospores are laid down

⁶ Zickler, H. Über künstliche erzeugung von Mikrohaplonten von Ascomyzeten. Biol. Centralb. 51: 540–546. 1931.

⁷ See footnote 2.

from the cytoplasm, no doubt as influenced by genes, now carried in the nuclei of the spore, now carried in the 16 nuclei distributed in the cytoplasm of the indurated ascus. All asci of *Neurospora* have an elastic ring-pore at the apex. This is a mechanism which has a function in the violent discharge of the ascospores.

Cultures obtained from indurated asci which were homozygous *dd* gave perithecia with asci which in turn, especially on corn meal agar, showed the deliquescent type of abortion. This proved that the factors *A*, *a* for sex reaction, as well as the recessive lethal *d* factor had been passed on to the f_1 races, now heterocaryotic because they had arisen through outgrowths from a heterocaryotic ascus. We have attempted to induce the deliquescent type of aborted asci to "germinate," but as yet with no success. Theoretically they could not do this because their eight nuclei have already gone through the first stages of degeneration. The sixteen nuclei in an indurated ascus persist for some time.

As noted in a previous paper⁸ such an ascus does occasionally delimit a few abnormal spores on spore-like bodies. Some asci from our recent matings of new races, each carrying the lethal *d*, at times did cut out rather abnormal-looking spores. We have found that some of them can be germinated (fig. 1, C). Cultures from such ascospores usually produced ascocarps, which always had aborted asci. Such ascospores would be perfectly satisfactory for analyzing the genetic factors represented in an ascus, provided one obtained three or four bisexual spores from the same ascus. It is believed, however, that one could more certainly obtain all the inheritance or component nuclei resulting from reduction by working with an indurated ascus. In either case the final step in continuing the breeding experiment would be to separate out the individual component f_1 races either by plating out conidia or microconidia, or by isolating single hyphal tips.

The senior author some years ago, while working with cultures of *Pezizella Lythri*, found that one could obtain "germination" or growth from the penultimate cell of the ascus crossier. Where this occurred one could see plainly that the young ascus was just beginning to develop. Since nuclear fusion occurs very early, or before the ascus elongates to any extent, it may be that we were seeing germination of a cell which was still diploid! Or it may be that reduction was occurring at germination, a sort of reversion to a primitive type in which the zygote reduces at germination. More likely, however, nuclear fusion had not yet taken place. Miss Angie Beckwith, who undertook to continue this work, later reported personally that she obtained what seemed to be perfectly normal mycelia from such proliferating ascus cells or primordia, and that normal conidia were later developed in her cultures.⁹

⁸ See footnote 1.

⁹ Unpublished work.

The particular importance of this kind of germination is that it results in the production of heterocaryotic mycelia. We find in recent literature the statement that a dicaryotic cell of a rust or of a mushroom is in fact diploid because the genes carried in each of its two haploid nuclei operate just as they would if they were included in the same nuclear membrane. The authors of such statements should realize that when the two haploid nuclei of a rust dicaryon fuse, so that all their genes are included within the same membrane, a mature teliospore results. When the two haploid nuclei in the mushroom dicaryon fuse so that their complementary genes are now within the same membrane, a basidium is formed. So it is clear that the manifestations of genes carried in the haploid nuclei of a dicaryon cannot possibly be the same as they are when drawn together within the same membrane of a diploid nucleus. What we should emphasize and insist on is that when the vegetative structure of a fungus contains two or more kinds of haploid nuclei, the effect, physiologically and morphologically, is the resultant of the combined, or the complementary, effects of all the genes working in the same cytoplasm. Complementary genes may be located in the same haploid nucleus or in two different haploid nuclei in the same cytoplasm. In such case we can say without fear of contradiction that it does not make any difference whether these genes are in the same nuclear membrane or not,¹⁰ so long as we do not bring them together through a nuclear fusion. This is quite different from saying that a dicaryotic cell, because it contains two haploid nuclei, is diploid, and that it can be heterozygous or homozygous as the case may be. It is still a dicaryotic cell, and it can be heterocaryotic or homocaryotic as the case may be.

It remains to discover just what cultural conditions result in indurated ascus abortion, without the intervention of the dominant lethal *I*. Some such method as that described by Zickler would be effective; or it may be that high temperatures during certain critical stages in the development of the asci would yield the same result. This is a problem requiring a more extensive study, but it will be worth while if one wishes to pursue either morphological, physiological, or genetical studies on heterocaryotic structures of *Neurospora*.

SUMMARY

Asci of types of *Neurospora tetrasperma* homozygous for *dd* abort and usually deliquesce without ascospore formation. This fact prevents breeding beyond the first (F_1) asci if both parents in the matings carry this recessive lethal, *d*. Deliquescent ascus abortion is due to the degeneration of the eight nuclei without spore delimitation. Certain cultural or other environ-

¹⁰ Dodge, B. O. Heterocaryotic Vigor in *Neurospora*. Bull. Torrey Club 69: 75-91. 1942. Reports from Recipients of Grants from the Research Funds. Year Book Am. Phil. Soc. 148-150. 1942.

mental conditions may, however, prevent nuclear degeneration, with the further result that a fourth division occurs. The ascus with 16 nuclei is marked by a thickened, brown, and striated ascus wall. Such asci resemble somewhat giant ascospores. When they are heated to 60° C for one hour, many of them will germinate. A way is thus provided for breeding generation after generation with the recovery of all the different types of nuclei coming from each mating even though the asci regularly abort. Occasionally in certain races a homozygous ascus (*dd*) does cut out one or two abnormal spores. Such spores can also be germinated, but one is not sure of recovering all four possible types of nuclei from an ascus.

THE NEW YORK BOTANICAL GARDEN
NEW YORK

STUDIES IN DREPANOCLADUS—I.¹

History, Morphology, Phylogeny, and Variation

FRANCES E. WYNNE

HISTORICAL ACCOUNT OF THE GENUS

Although the name *Drepanocladus* was not proposed until 1851, several of the species included were described under *Hypnum* by Hedwig and previous workers. It is therefore necessary to trace the concept of the genus *Drepanocladus* from the beginning of bryological nomenclature.

In his fundamental work, *Species Muscorum*, Hedwig (1801), included only three of the species now placed in *Drepanocladus*—*Hypnum aduncum*, *H. fluitans* and *H. uncinatum*. Turner (1804) in his *Spicilegium* considered these three and added *Hypnum revolvens*. Bridel (1812), in the second supplement of *Muscologia Recentiorum*, added *Hypnum lycopodioides*.

As early as 1827 the species of *Hypnum* with unicostate, falcate-secund leaves were recognized as a unit and, in this *Bryologia Universa*, Bridel (1827) segregated them under the heading, which may be interpreted as a section, "Adunci." In this work he placed 65 of the species of *Hypnum* in the subgenus *Stereodon*; 8 of these are included under "Adunci." He does not state that *Stereodon* is a subgenus but it is not numbered in the series with the genera so cannot be considered a genus. That he was familiar with the concept of the subgenus is evidenced by the statement in the preface: "Sic genus *Campylopus* melius instituimus, speciebus omnibus quae calyptra mitriformi utuntur ab illo detractis et in genus novum nobis *Dryptodon* dictum quodque *Grimmium* tanquam subgenus continuat, conflatis." The species included under "Adunci" are *Hypnum Stereodon aduncus*, *fluitans*, *uncinatus*, *lycopodioides*, and *scorpioides* with three other species still in *Hypnum* and one species now in *Hylocomium*.

In his *Synopsis Muscorum*, Müller (1851) further segregated these species into section *Mallacodium* and created the name *Drepanocladus* for the subsection which included *H. riparium* (now in *Leptodictyum*), *H. uncinatum*, *H. fluitans*, *H. aduncum*, *H. revolvens*, and *H. paradoxum*.

The first monographic treatment of the present species of *Drepanocladus* appeared in the *Bryologia Europaea* (1854, 1866) where the group was treated as Section VII of *Hypnum* under the descriptive heading: "Caulis erectus vel prostratus, folia falcato-secunda, unicostata." To the species earlier considered were added *H. exannulatum* in the monograph and *H.*

¹ This is the first of a series of four articles on *Drepanocladus*; the others will appear in BRITTONIA, THE AMERICAN MIDLAND NATURALIST, and THE BRYOLOGIST.

Cossoni, *H. Sendtneri*, and *H. vernicosum* (described first in 1861 by Lindberg) in the first supplement. Our present species *Drepanocladus Kneiffii* appeared first in the *Bryologia Europaea* under the genus *Amblystegium*. All the species are described with the completeness and accuracy and illustrated with the beauty characteristic of the *Bryologia Europaea*.

Bridel's recognition of the group "Adunci" was followed by subsequent workers in *Hypnum*. In *The Musci and Hepaticae of the United States* Sullivant (1856) proposed the subgenus *Harpidium* to include essentially the same species, namely, *Hypnum aduncum*, *H. uncinatum*, *H. revolvens*, and *H. fluitans*. Schimper, in his two editions of *Synopsis Muscorum Europaeorum* (1860, 1876) placed in the subgenus *Harpidium* *Hypnum Kneiffii*, *H. aduncum*, *H. lycopodioides*, *H. crannulatum*, *H. fluitans*, *H. revolvens*, *H. uncinatum* (in ed. 1), and *H. vernicosum*, *H. Cossoni*, *H. Sendtneri*, *H. hamifolium*, *H. pseudostramineum*, and *H. Molendoanum* (in ed. 2).

De Notaris (1838) in his *Syllabus Muscorum* included *H. scorpioides*, *H. lycopodioides*, *H. aduncum*, *H. fluitans*, and *H. uncinatum* with several other species of *Hypnum* in Section "Adunca" of *Hypnum*. However in his *Bryologia Italiana* (1869) he transferred the following species to *Amblystegium* II *Macrophylla* (which included also several present species of *Amblystegium* and *Hypnum*): *H. Rotae*, *H. lycopodioides*, *H. Sendtneri*, *H. revolvens*, *H. fluitans*, *H. uncinatum*, *H. exannulatum*, and *H. Kneiffii*.

Hartman and Lindberg, in Hartman's *Skandinavien Flora* (ed. 5, 1849; ed 8, 1861; and ed. 9, 1864) proposed the new species *Hypnum badium*, *H. vernicosum*, and *H. intermedium* but did not add, in their floristic treatments, anything new to the concept of the group as a whole.

By 1869 the concept of the genus *Drepanocladus* as we know it today was well defined and most of our present species had been described. The process until this time had been to describe the species and to group them according to their relationships. Beginning in 1880 with Sanio's work a tendency developed to split this small group of species into many species, subspecies, varieties, and forms. The present genus *Drepanocladus* was shifted from *Amblystegium* to *Hypnum* and back again several times during this period.

Carl Sanio, in numerous papers from 1880-1887, treated the group as the subgenus *Harpidium* of *Hypnum*.² His classification, following a

² *Commentatio de Harpidiis europaeis inductiva*. Bot. Centralbl. 1880 (Beilage 2): 1-24. 1880. *Additamentum in Hypni adunci cognitionem*. Bot. Centralbl. 5(3): 93-95. 1881. *Additamentum secundum in Harpidiorum cognitionem*. Bot. Centralbl. 13(13): 425-440. 1883. *Beschreibung der Harpidien, welche vornehmlich von Dr. Arnell während der Schwedischen Expedition nach Sibirien im Jahre 1876 gesammelt wurden*. Sv. Vet.-Akad. Handl. 10(1): 1-62. 1885. *Bryologische Fragmente*. Hedwigia 26: 99-109; 129-169; 194-214. 1887.

typographically complicated system of Greek and Roman letters and numerals, indentations, asterisks, and daggers, is obscure and difficult to interpret. He described many new species, varieties, and forms, and gave formal recognition to every possible minor habitat variation. Although some of his descriptions are long and detailed, others are extremely meager and all are without definite measurements of any kind. Fortunately, most of his names have never been used for American plants, and so they need not be included in the synonymy here.

Boulay's treatment of Section *Harpidium* of *Hypnum* in *Muscinées de la France* (1884) was original and complete and the best monographic treatment of the group since the *Bryologia Europaea*. He collected the many scattered references to numerous species which had been proposed in the journals and pamphlets between 1866 and 1884 and put the material into workable form. His work is good because of its full detailed descriptions, excellent habitat notes, and comments on diagnostic features and relationships. With each revision of the group, more varieties appeared, and Boulay, no exception, proposed numerous new ones to add to the already long list.

Renauld's greatest contribution to the concept of the genus *Drepanocladus* was his indication of a variety or forma "typicum" for *Hypnum aduncum*, *H. fluitans*, and *H. revolvens*. Previously, no one had ever indicated the concept of a "typical" plant, which was rapidly being lost in the maze of varieties. I think it is safe to say that the modern concept of the genus begins with Renauld's work. His revision of Section *Harpidium* of *Hypnum* in Husnot's *Muscologia Gallica* (1894), supplemented by his numerous smaller papers,³ is extremely useful; as much for its notes of habit and relationships and its illustrations as for its taxonomic revision. His use of the ambiguous category "groupe" and "sous-groupe" often makes his nomenclature and classification obscure. Renauld retained many of Sanio's and Boulay's names and created many new, inadequately described varieties and forms.

Between 1875 and 1918 numerous local floras included treatments of the present genus *Drepanocladus*. In Berggren's *Musci et Hepaticae Spetsbergenses* (1875) several new varieties were proposed for these species, which he included under *Hypnum*. Lange and Jensen (1887) in their treatment of *Harpidium* in *Conspectus Florae Grønlandicae* gave full generic recognition to what had previously been a subdivision of *Hypnum*. The group, with new species, was included with *Amblystegium* by Lindberg and Arnell (1890) in *Musci Asiae Borealis* and Arnell and Jensen (1907) in *Die Moose des Sareckgebietes*. However, Bryhn (1906) in reporting the bryophytes of

³ Classification systématique de la section *Harpidium* du genre *Hypnum* de la flore française. *Rev. Bry.* 8: 73-82. 1881. Causerie sur les *Harpidia*. *Rev. Bry.* 33: 89-100. 1906; 34: 7-14. 1907. Notes sur quelques *Drepanocladus*. *Rev. Bry.* 36: 129-138. 1909; 37: 29-34. 1910.

the second expedition of the "Fram" and Hesselbo (1918), in *The Bryophyta of Iceland*, both considered the species in *Hypnum*.

The American publications of this period (Lesquereux and James' *Manual of the Mosses of North America* (1884) and Kindberg in Macoun's *Catalogue of Canadian Plants* (1892)) treated the group as the subgenus *Harpidium* of *Hypnum*.

Limpricht (1897-1898) in *Die Laubmoose Deutschlands, Oesterreichs, und der Schweiz*, includes 19 species in *Hypnum*, subgenus *Drepanocladus*, with full descriptions and measurements, and detailed distribution notes. Although every species is not illustrated, the pictures provided are clear and helpful.

Although Müller is responsible for the name *Drepanocladus*, Warnstorf, in his article "Die Europäischen Harpidien" was the first to use it as a genus and make the combinations.⁴ His article is important because of its comprehensive treatment which includes many new combinations as well as a historical survey of the literature, a general discussion of the relationships of the species, a key to the species, descriptions, and the distribution. Warnstorf (1906) followed his excellent and useful monograph with an equally fine treatment of *Drepanocladus* in *Kryptogamenflora der Mark Brandenburg*. His keys and descriptions are complete and detailed but of his 24 species, only 7 can be recognized as valid species; the remainder of his names have been reduced to either varieties or synonyms. Not only did he divide the genus into many species, but also he included innumerable varieties for each species. He, like Boulay, Renauld, and Limpricht, was a "splitter."

Roth (1905) in *Die Europäischen Laubmoose* treats 22 species of *Drepanocladus* with full descriptions, citations, and references. His treatment resembles Warnstorf's in that over half of his species are today recognized as merely varieties or habitat phases.

Loeske⁵ in an article "Drepanocladus, eine biologische Mischgattung" discussed the morphology of the group and its relationship to closely related genera and proposed the following names as genera. Although he indicated the species to be included, his new genera are *nomina nuda*, since he gave no descriptions of them.

1. *Sanionia*—*uncinata*, *orthothecioides*, *contigua*.
2. *Limprichtia*—*vernica*, *intermedia*, *revolvens*.
3. *Warnstorfia*—*exannulata*, *orthophylla*, *tundrac*, *purpurascens*, *fluitans* and varieties.
4. *Drepanocladus*—*aduncus* and varieties.
5. *Pseudocalliergon*—*turgescens*, *trifarum*, *longicuspis*.
6. *Scorpidium*—*scorpidioides*.

⁴ Beih. Bot. Centralbl. 13: 338-430, 1903.

⁵ Hedwigia 46: 300-321, 1907.

In his *Studien zur vergleichenden Morphologie und phylogenetischen Systematik der Laubmoose* (1910) he discusses these groups in more detail and supplements his statements of relationships among the species in the group. However, his names are still without generic descriptions.

Mönkemeyer's treatments of *Drepanocladus* in Pascher's *Süßwasser-Flora* (1914, 1931) and in *Die Laubmoose Europas* (1927) initiated the present tendency to reduce the number of species in the genus. There is no essential difference among his three publications; each includes the same eight species with keys, illustrations, and descriptions. Although he decreased the number of species, he included a large number of varieties and forms under each.

Brotherus, in "Die Laubmoose Fennoskandias" (1923) and in *Die natürlichen Pflanzenfamilien* (1925) adopted Mönkemeyer's policy of reducing the number of species and followed in large part his arrangement of varieties and forms. He used Loeske's proposed genera as sections and added section *Pseudo-Drepanocladus* for *Hypnum badium* Hartman.

Although writing as late as 1924, in *The Student's Handbook of British Mosses*, Dixon still included the species of *Drepanocladus* in *Hypnum*, subgenus *Harpidium*. His treatment follows Renauld's monograph with slight differences. The comments on distinguishing features, inter-specific and inter-variatal relationships, and habitats are his most valuable contribution.

The most recent treatment of *Drepanocladus* is Grout's in *Moss Flora of North America* (1931). As he states in his introduction, he has based his work on Renauld's and Mönkemeyer's published monographs and on their identified specimens.

As has been seen from the preceding synopsis, the concept of the genus *Drepanocladus* developed in Europe and most of the type localities are European. Because most of the species were described before the type concept was developed, types have never been designated. Under present world conditions it has been impossible to borrow material from Europe. However, the concept of the species has been so well developed in European and American literature and American herbaria that it has been possible to interpret American material from the descriptions, illustrations, and specimens. Because of the impossibility of studying European types and herbarium material, I have been forced to confine the scope of this monograph to North America. Therefore, only American material and names have been included; names which have never been used for American plants have not been considered.

MORPHOLOGY

Habit. The variability of *Drepanocladus* in habit, branching, and size depends largely on habitat conditions. *Drepanocladus uncinatus*, which most

frequently creeps over the ground, logs, or rocks, is irregularly or regularly pinnately branched. The stems of *D. aduncus* when growing among grass or reeds in swamps and marshes are creeping and fastigiately or irregularly pinnately branched. Submerged, floating stems are usually long, but may be either simple or regularly pinnately branched. Large, plumose fronds result when the stems are pinnate in the aquatic phase of *D. aduncus*, *D. fluitans*, or *D. exannulatus*. *D. uncinatus* var. *subjulaceus*, *D. exannulatus*, *D. brevifolius*, and *D. badius* often grow 5–8 cm. high, their stems erect, and simple or fastigiately branched. In bogs, *D. vernicosus*, *D. revolvens*, *D. aduncus*, *D. fluitans*, and *D. exannulatus* grow suberect in tufts and are fastigiately or irregularly pinnately branched. Sudden changes in environmental conditions may produce several long branch innovations near the tips of the stems.

Color. Although color is variable in *Drepanocladus*, it is reasonably characteristic for each species. *D. uncinatus* is from shining golden to yellow-green; *D. vernicosus* is light yellow-green; *D. aduncus* is from yellow-green to grass-green; *D. fluitans* is from dull yellow-green to brown; *D. exannulatus* is from crimson to red or purple; *D. revolvens* is from green to deep red or black and has a metallic sheen; *D. brevifolius*, *D. badius*, and *D. lycopodioides* are deep golden at the growing tips and brown or black below.

Stems. The apical buds of stems and branches are always pointed and are usually falcate-secund (except in *D. aduncus* var. *Kneiffii* and depauperate forms of *D. exannulatus*). However, in *Drepanocladus*, the apical buds are never cuspidate as is characteristic in the closely related genus, *Calliergon*.

The stems of *Drepanocladus* generally lack paraphyllia and radicles. Pseudoparaphyllia are produced in the axils of the branches of *D. uncinatus*. Some plants of *D. fluitans* and *D. badius* produce radicles from the apex, base, margin, or costa of the leaves.

The stems of all the species of *Drepanocladus* (except *D. vernicosus* in which the central strand is lacking) show in cross section a small central strand of 3–6 cells embedded in a loose ground tissue. The 2–3 rows of cortical cells may or may not be incrassate or colored. The outer layer of cortical cells of *D. revolvens* is enlarged. Stems vary in diameter from 2–6 mm.

Leaves. Although the leaves of *Drepanocladus* are typically falcate, and may further be strongly and regularly circinate (*D. uncinatus* and *D. revolvens*), they are straight in *D. aduncus* var. *Kneiffii* and the short-celled environmental phases of *D. fluitans* and *D. exannulatus*. In submerged

plants the curvature of the leaves is decreased and the acuminations are long, lax, and twisted. The strongly falcate leaves of *D. aduncus*, *D. fluitans*, and *D. exannulatus* are channelled at the apex, whereas the straight leaves of some of their varieties have a flat apex.

The leaves of *Drepanocladus* range from strongly and regularly plicate, through irregularly plicate and striate, to completely plane. *D. uncinatus* is the only species of the genus with strongly regularly plicate leaves; the plications are distinctive because each fold extends continuously from the base of the leaf to the apex. The leaves of *D. vernicosus* are plicate only in the broadened basal part, with the apex flat. Forms of other species (*D. exannulatus*, *D. fluitans*, and *D. aduncus*) may become irregularly striate or sulcate in response to certain environmental conditions. This and similar characters, resulting from habitat conditions, are usually not constant on any plant. In the other species, *D. revolvens*, *D. lycopodioides*, *D. badius*, and *D. brevifolius*, the leaves are not folded in any way; they are plane or concave.

The shape of the leaves of *Drepanocladus* varies from broadly oval to linear-lanceolate. Leaves of small plants of *D. aduncus* are broadly ovate; leaves of *D. aduncus* var. *Kneiffii*, *D. badius*, *D. lycopodioides*, *D. brevifolius*, *D. fluitans*, and *D. exannulatus* are broadly lanceolate; leaves of *D. exannulatus* and aquatic plants of *D. aduncus* are long lanceolate; leaves of aquatic plants of *D. fluitans* are linear-lanceolate.

The acumination may be short and abrupt or long and gradual. Half the length of the leaf of *D. uncinatus* is the long, subulate acumen. The acumination of *D. vernicosus* is abrupt and broad. The leaf of *D. revolvens* is gradually narrowed until within 0.3–0.5 mm. of the apex where it is rapidly narrowed to a filiform point. Forms with ovate or broadly lanceolate leaves are usually abruptly short-acuminate whereas forms with long-lanceolate or linear-lanceolate leaves are gradually long-acuminate. In general, long leaves with long acuminations are produced by complete submergence.

The leaves of all the species of *Drepanocladus* clasp the stem, and are erect rather than spreading. The alar region of the leaf may or may not be decurrent. As a result of variation in decurrency, the line of insertion of the leaf varies from truncate, through broadly or narrowly concave to circular. The alar cells of *D. aduncus* are decurrent, therefore the base of the leaves is always concave. Whether the line of insertion is widely or narrowly concave depends upon the width of the leaf at the base, the diameter of the stem, and the degree of decurrence of the alar cells. Since the alar cells of *D. fluitans* and *D. exannulatus* are not decurrent, the base of the leaf is truncate. The few quadrate alar cells of *D. uncinatus* are slightly decurrent, thus forming a shallowly concave line of insertion seen when the leaves are

removed from the stem. Leaves of *D. revolvens*, *D. badius*, *D. vernicosus*, *D. brevifolius*, and *D. lycopodioides* with quadrate cells across the entire base are always truncate.

The margin of the leaves of *D. aduncus*, *D. vernicosus*, *D. revolvens*, *D. lycopodioides*, *D. badius*, and *D. brevifolius* is entire or sinuate at the base. The leaf margins of *D. exannulatus* and *D. fluitans* are serrulate at the base or apex or both. The long subulate acumination of *D. uncinatus* is distinctly serrulate while the base is entire or only slightly serrulate. Whether the serrulations are distant or close depends upon the length of the cells.

Costa. The leaf costa or nerve of *Drepanocladus* is almost universally single, not forking or double (except in *D. fluitans* var. *Berggrenii*); it varies in length and width. In depauperate forms of *D. aduncus* and *D. fluitans* it is short ($1/3$ – $1/4$ the length of the leaf) and weak (12 – $20\ \mu$ in diameter at base). In *D. vernicosus*, *D. uncinatus*, *D. revolvens*, *D. exannulatus*, and *D. fluitans* it is long ($1/2$ – $5/6$ the length of the leaf) and strong (40 – $80\ \mu$ wide at the base). In *D. aduncus* var. *capillifolius* and *D. exannulatus* var. *Rotae* the costa is long-excurrent and 80 – $150\ \mu$ wide at the base, and usually deeply colored. Submerged plants of *D. aduncus* and *D. exannulatus* may develop a wide, deeply colored costa. In all species of *Drepanocladus*, including the varieties with excurrent costa, it is tapering.

The cells of the costa are narrowly linear, and usually longer than the cells of the lamina of the leaf. With the exception of *D. vernicosus*, the costa as seen in cross-section is biconvex with a small central strand. The costa of *D. vernicosus*, like the stem, has no central strand.

Arcolation. The leaf cells of *Drepanocladus* are narrowly linear, with the exception of certain habitat phases of *D. aduncus*, *D. fluitans*, and *D. exannulatus*, in which the median leaf cells are oblong (4 – $6\ \mu \times 28$ – $32\ \mu$). Cells are longest in *D. fluitans* and *D. exannulatus* (4 – $6\ \mu \times 60$ – $100\ \mu$) and shorter in *D. aduncus*, *D. revolvens*, *D. vernicosus*, and *D. uncinatus*. In general the cells are uniform in size and shape throughout the leaf, being only slighter shorter and broader toward the base in *D. aduncus*.

The cell walls are thin in *D. aduncus*, *D. fluitans*, *D. uncinatus* and *D. vernicosus*. In some plants of *D. exannulatus* and *D. aduncus* the walls of basal and alar cells are deeply colored. Basal cells of *D. revolvens* and *D. lycopodioides* are pitted, whereas all cell walls in *D. badius* and *D. brevifolius* are porose. In *D. revolvans* only the basal cell walls are incrassate; in *D. badius* and *D. lycopodioides* all cell walls are incrassate and deeply colored brown or red.

The alar cells of *Drepanocladus* may be large and inflated, small and quadrate, hyaline or colored, thin-walled or incrassate, entire or porose, or any combination of these. In *D. aduncus* the alar cells are inflated and

hyaline, forming distinct auricles extending $1/4$ – $1/3$ the distance from the margin to the costa. Only in extremely robust submerged plants are the basal and alar cells colored in *D. aduncus*. In *D. fluitans* the alar cells are slightly inflated and extend $1/4$ – $1/3$ the distance from the margin to the costa. The alar cells of *D. exannulatus* are always large, but may be thin-walled or incrassate, hyaline or colored, and form either large triangular groups extending to the costa or a single row of elongated cells across the entire base. The alar cells of *D. badius* are inflated, incrassate, and porose. *D. uncinatus* has a small group of quadrate, hyaline alar cells. The alar cells of *D. vernicosus*, *D. revolvens*, *D. lycopodioides*, and *D. brevifolius* are not differentiated at the basal angles, although there are two or more rows of shorter cells (hyaline and thin-walled in *D. vernicosus*; incrassate, porose, and colored in *D. revolvens*) across the entire base of the leaf. In general, if the alar cells are large and inflated they are thin-walled; and if they are incrassate they are smaller.

The incrassate cell walls between any two basal cells of *D. revolvens* are $4\ \mu$ thick, usually with 1–3 pits. The two secondary cell walls between two alar cells are 4 – $8\ \mu$ thick in *D. revolvens*, *D. badius*, and *D. lycopodioides*.

Alar cells differ not only in their size and shape but also in their spatial relationship with the other cells of the leaf. The alar cells of *D. aduncus* and *D. fluitans* intergrade completely with the cells of the lamina of the leaf and the transition is imperceptible. However, in *D. aduncus* the alar cells are ventricose and oriented in a different plane from the other leaf cells so that the alar cells are sharply delimited from the cells of the lamina. The alar cells of *D. exannulatus* and *D. fluitans* are never ventricose nor placed at an angle. *D. exannulatus*, unlike *D. fluitans*, shows an abrupt transition from the alar cells to the cells of the lamina so that the alar region is sharply delimited by the size of the cells.

When leaves of *D. fluitans*, *D. exannulatus*, and *D. aduncus* are removed from the stems, usually some of the cortical stem cells remain attached to the base of the leaves as long "tails." This does not occur so often in *D. vernicosus*, *D. uncinatus*, *D. revolvens*, *D. badius*, *D. brevifolius*, or *D. lycopodioides*. One of the differences distinguishing *D. aduncus* from *D. fluitans* and *D. exannulatus* is the transition from the stem cells to the leaf cells; in *D. aduncus* it is gradual, whereas in *D. fluitans* and *D. exannulatus* it is abrupt.

Perichaetium. In all species of *Drepanocladus* the perichaetium sheaths the base of the seta. The outer perichaetial leaves are spreading, from ovate to broad-lanceolate, and either ecostate or with a short costa. The inner perichaetial leaves are costate, long-lanceolate, and from gradually or abruptly acuminate to piliform. The perichaetial leaves of *D. uncinatus*, like the vegetative leaves, are regularly and strongly plicate and serrulate at the

apex. In other species, the perichaetial leaves are smooth or irregularly striate, and entire or serrulate.

Perigonial leaves. The perigonial leaves of all species of *Drepanocladus* are similar. They are ovate, abruptly short-acuminate, with a short costa or ecostate, serrulate or entire.

Sporophyte. The capsule and peristome of *Drepanocladus* are typically Hypnaceous. With the exception of the erect symmetric capsule of *D. uncinatus* var. *symmetricus*, the capsule of all species is asymmetric and curved; it may be plicate or smooth. The exothecial cells are smooth or mamilllose. The operculum is rostrate or apiculate, attached in all species (except *D. fluitans* and *D. exannulatus*) by a persistent annulus of 2–3 rows of cells. The peristome is perfect, that is, with sixteen teeth and sixteen segments and alternating cilia. The sixteen teeth are transversely thickened and longitudinally striate. The segments of the inner peristome are longitudinally striate with 2–3 cilia.

PHYLOGENY

Drepanocladus belongs to the subfamily Amblystegieae, which includes all the Hypnaceae which have a single costa and a long arcuate-cylindric capsule.

Generic relationships. *Drepanocladus* is most closely related to *Scorpidium*; in fact, the relationship is so close that they have been grouped together by many bryologists. One species of *Scorpidium* is recognized today—*S. scorpioides*. Milde⁶ placed it in the subgenus *Harpidium* with the present species of *Drepanocladus*, and Warnstorf⁷ called it *Drepanocladus scorpioides*. *Scorpidium* has all the characteristics of the genus *Drepanocladus* except that the leaf apex is obtuse or apiculate and the costa is faint, short and double, or lacking. To the naked eye, the two genera are so similar that *Scorpidium scorpioides* resembles a very large *Drepanocladus*.

Although *Calliergon* differs from *Drepanocladus* in its straight leaves and rounded or cucullate apices, the close relationship between the two genera is shown not only in their similarity of areolation and costa, but also by their parallel series of species. The same modifications of alar cells, cell walls, costae, and leaves that separate the species of *Drepanocladus* likewise distinguish the species of *Calliergon*. The two genera occur in the same range and in the same types of habitats and are often found associated.

Calliergidium, intermediate between *Drepanocladus* and *Calliergon*, seems to be an artificial genus. One of its species, *C. pseudostramineum*, is

⁶ *Bryologia silesiaca*, p. 350. 1869.

⁷ *Kryptogamen-Flora der Mark Brandenburg und angrenzender Gebiete*. 2: 1027. 1906.

so closely related to *Drepanocladus* that Warnstorf⁸ and Brotherus⁹ have considered it a form of *D. fluitans*. Grout¹⁰ has considered the erect and straight leaves with blunt apices sufficiently distinctive to separate *C. pseudostramineum* from *Drepanocladus*. In general habit, the plants named *D. pseudostramineum* I have seen have resembled *Calliergon* more than *Drepanocladus*. Further collections of these two species, will, I believe, dispense with this artificial genus and place its species in *Drepanocladus* and *Calliergon*.

In a phylogenetic arrangement, *Drepanocladus* and *Calliergon* form a related species-complex to which the other members of the subfamily are less closely allied.

The species of *Hygrohypnum* with falcate, acuminate leaves and a single costa superficially resemble the species of *Drepanocladus*. However, the species with straight, blunt leaves and short, double costae are never confused with *Drepanocladus*. Furthermore, *Hygrohypnum*, *Hygroamblystegium*, and *Leptodictyum* grow most frequently in running water, whereas *Drepanocladus* occurs usually in still water. *Hygrohypnum* is so variable and heterogeneous a group that it is difficult to determine its relationship to other genera.

Cratoneuron, in spite of its falcate leaves, decurrent alar cells, and single costa, is distinctive from *Drepanocladus* because of its numerous paraphyllia. It is the only genus in the subfamily which has developed paraphyllia and it therefore holds a unique place in the phylogeny of the Amblystegiaceae.

Hygroamblystegium is separated primarily from *Amblystegium* on the basis of its aquatic habitat. On the same basis it is more closely allied to and more often confused with *Drepanocladus* than is *Amblystegium*. However, any similarity between *Hygroamblystegium* and *Drepanocladus* is only superficial, for the robust habit, erect-spreading, non-falcate leaves, and thick-walled rhomboidal leaf cells distinguish *Hygroamblystegium*.

Leptodictyum, like *Hygroamblystegium*, resembles *Drepanocladus* only superficially in its aquatic habitat. The leaves are never falcate, but are always erect or erect-spreading, and the alar cells are never inflated. These characters distinguish species of *Leptodictyum* from *Drepanocladus aduncus* var. *Kneiffii*, the only *Drepanocladus* to which it shows any similarity.

Plants of *Amblystegium* or *Campylium* with falcate leaves are sometimes confused with small plants of *Drepanocladus*. *Campylium*, with its typically squarrose-recurved, broadly ovate or lanceolate leaves, is unlike any species or variety of *Drepanocladus*. *Amblystegium* is distinct in its short leaf cells, erect-spreading leaves, and quadrate or only slightly inflated alar cells.

⁸ L.c., p. 1040.

⁹ Die Laubmoose Fennoskandias 1: 479, 1923.

¹⁰ Moss flora of North America north of Mexico 3(2): 100, 1931.

Interspecific relationships. The origin of the species of any group is a speculative but nevertheless an interesting and significant problem. From the comparative morphology of the species of *Drepanocladus*, it is possible to deduce the relationships and to postulate the origin of the species of the genus.

Two general trends of development in the genus have been (1) the production of inflated cells, and (2) the production of alar cells which are not inflated, but which may be differentiated in other ways (see figure 1).

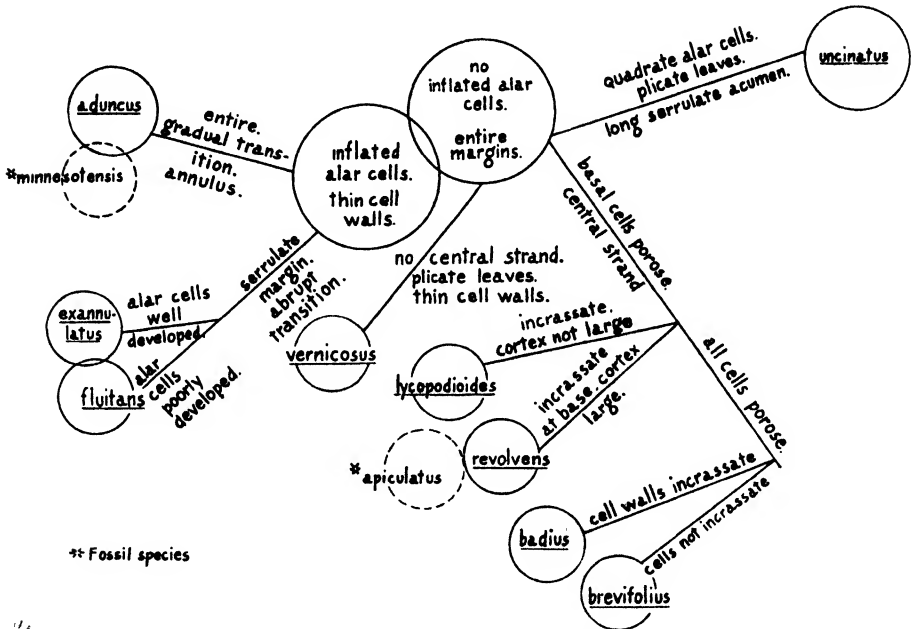


FIG. 1. Inter-relationships of the species of *Drepanocladus*.

Drepanocladus aduncus, *D. fluitans*, and *D. exannulatus* have inflated alar cells and are obviously closely related. An early ancestor must have furnished to all three species the inflated alar cells, and thin cell walls which are not pitted. Subsequent segregation of traits gave rise to (1) *D. aduncus* with entire margins and a gradual transition from the cortical stem cells to the leaf cells, and to (2) *D. fluitans* and *D. exannulatus* with serrulate margins and an abrupt transition from cells of the stem to the cells of the leaf, and the annulus lacking on the capsule. Further evolution has segregated *D. fluitans* with its delicate habit and its poorly developed alar cells which intergrade completely with the cells of the lamina, and *D. exannulatus* with its robust habit and its well developed, clearly delimited alar cells extending across the entire base of the leaf.

Development of the three species, *D. fluitans*, *D. exannulatus*, and *D. aduncus* must have been parallel, because the series of varieties in each is

similar. These three species respond to the same environmental conditions with the same modifications. Each species when growing submerged produces longer stems, longer leaves at greater intervals on the stems, longer leaf cells, and regular pinnate branching. Each species also produces a short-celled, short-leaved phase when it grows in certain unfavorable conditions. Although the variety with an excurrent costa is lacking in *D. fluitans*, it is present in both *D. aduncus* (var. *capillifolius*) and *D. exannulatus* (var. *Rotae*). *D. aduncus*, unlike *D. fluitans* and *D. exannulatus*, produces a variety with straight leaves (var. *Kneiffii*).

The other evolutionary trend, the production of alar cells which are not inflated, gave rise by various combinations of characters to the other species of the genus. Any postulation of the order in which these forms were produced would be pure speculation. *D. vernicosus*, *D. revolvens*, *D. brevifolius*, and *D. lycopodioides* are similar in the absence of any differentiated cells at the basal angles of the leaf, and in the presence of several rows of differentiated cells across the entire leaf base. *D. vernicosus*, the only species in the genus without a central strand, is distinct in its stem structure, and in its characteristically plicate and abruptly acuminate leaves with thin-walled cells.

Drepanocladus revolvens and *D. lycopodioides* may have developed from the same stock. *D. revolvens* has only the basal cells incrassate and pitted, whereas, in *D. lycopodioides*, all the cell walls are incrassate with the basal cell walls very thick and porose. The tendency toward incrassate, porose cell walls, partially developed in *D. revolvens*, is intensified in *D. lycopodioides*. The two species differ slightly in stem structure; the outer layer of cortical cells in *D. revolvens* is enlarged, whereas all the cortical cells are of the same size in *D. lycopodioides*. In habit and leaf shape the two species are similar except that *D. lycopodioides* is larger and more robust than *D. revolvens*.

Drepanocladus brevifolius and *D. badius* developed the same cell-wall modifications to produce plants in which all the leaf cells are porose. In *D. brevifolius* the cell walls are uniform in thickness and not, or only slightly, incrassate, whereas in *D. badius* all cell walls are incrassate with the basal cells especially strongly thickened. There are minor differences between the two species in the alar cells: in *D. brevifolius* there are no differentiated alar cells, but some leaves have a row of slightly inflated cells across the insertion of the leaf; *D. badius* always has some differentiated cells, either at the basal angles or across the entire base of the leaf.

Drepanocladus uncinatus is so distinct from all the other species of the genus that it seems probable that it developed along a separate line from the other members of the group. It has neither the inflated alar cells of *D. aduncus*, *D. fluitans*, or *D. exannulatus*, nor has it the basal row of dif-

ferentiated cells characteristic of *D. vernicosus*, *D. revolvens*, and *D. lycopodioides*. Instead, a group of quadrate alar cells is always present. The regular, long plications and the long, subulate, serrulate acumen are characteristic of *D. uncinatus*. Not only is *D. uncinatus* distinctive in its diagnostic features, but also in its habitat. It is the only species of *Drepanocladus* which is xerophytic or mesophytic rather than hydrophytic. In fact, *D. uncinatus* is so distinct that Loeske created the genus *Sanionia* for *D. uncinatus* and its varieties (see above).

From *D. uncinatus* developed the var. *symmetricus* with erect symmetric capsules but otherwise with the gametophytic characters of the species; this variety is restricted in its range to the western part of North and South America.

VARIATION IN DREPANOCLADUS

The species of *Drepanocladus* are well defined and have been known for a long time. On the other hand, the many forms and varieties which have been proposed for some of the species have been poorly defined and troublesome for taxonomists. I believe that lack of understanding of the variation in the genus is responsible for the taxonomic dilemma which confronts bryologists working in it.

Variation is of two sorts: that which is initiated by environment and that which is based on heredity. Botanists have confused these two types of variation in many groups of plants, including *Drepanocladus*.

American bryologists have recognized that species of *Drepanocladus* respond to changes in environment to a startling degree. Grout¹¹ states: "In 1929, in a pond not far from Cold Spring Harbor, was collected *Drepanocladus fluitans gracilis*. In 1931, when the water was low, there was a vigorous emergent growth, the upper leaves of which were typical *D. fluitans Jeanbernati*, while the lower leaves, grown apparently while submerged, were those of var. *gracilis*. On some of the shoots were leaves nearly typical of *D. fluitans* proper. This seems to show that in *Drepanocladus*, at least, habitat conditions modify structure profoundly." Conard¹² investigated the same pond in 1933 and 1934 and found the same conditions to exist: "In wet seasons this moss is the var. *gracilis*, but in dry seasons it becomes var. *Jeanbernati*." I have not recognized these two so-called varieties, *Jeanbernati* and *gracilis*, because they, along with many others, are merely environmental fluctuations.

Sporophyte characters are of little value in determining species of *Drepanocladus*. With the exception of *D. fluitans* and *D. exannulatus* which have no annulus on the capsule, and *D. uncinatus* var. *symmetricus* which

¹¹ Miscellaneous notes on mosses. *Bryologist* 36: 25, 26. 1933.

¹² The plant associations of Central Long Island—A study in descriptive plant sociology. *Am. Mid. Nat.* 16: 433-516. 1935.

has an erect instead of cernuous capsule, the sporophytes of all species of *Drepanocladus* are identical. Gametophyte characters, therefore, must be used for classification and identification. Great variation in habit, color, branching, leaves, costae, and areolation has led to the publication of many varietal and formal names for extreme plants produced by extreme environmental conditions. Because the most variable species of *Drepanocladus*, *D. aduncus*, *D. fluitans*, and *D. exannulatus*, have responded to different environments with similar modifications, a long series of variety and form names have been proposed for each of the species. Most of these subspecific names were first proposed under *Hypnum*; many of them were never transferred to *Drepanocladus*. Submerged plants of *D. aduncus* have been called var. *aquaticum*, *laxifolium*, *pseudofluitans*, and *laxum*; of *D. fluitans*, var. *submersum*; of *D. exannulatus*, var. *longifolium*. Small forms of these three species have been given variety and form names such as *gracilescens*, *tenue*, *attenuatum*, *filiforme*, *brevifolium*, *tenellum*, *condensatum*, and *abbreviatum*. Deeply colored plants have been called var. *purpurascens*. Short-celled leaves have been called *polycarpon* and *brachydictyon*. Every possible environmental variation has been named.

When the true nature of variation in *Drepanocladus* is understood, it is possible to eliminate these innumerable varieties which cannot be described nor recognized. The result of such a procedure is that only a few subspecific names remain and these are varieties which are hereditary.

In spite of the fact that bryologists have long recognized that much of the variation in *Drepanocladus* was due to environmental conditions, no attempt has heretofore been made to restrict varieties to hereditary variation. I have given varietal rank only to those variations which appear to be hereditary; environmental fluctuations have been discussed so that they may be recognized as such, but will not be included in the formal taxonomy. When a character is constant in all parts of a plant, regardless of environment, it is apparent that its uniformity is the result of fundamental genetic factors. When a certain character differs on different parts of the same plant—for instance, leaves from different parts of the stem—it is obviously influenced by environmental conditions.

Field and herbarium studies were made to determine which characters were modified by changes in the environment and which remained constant through a changing environment. It was discovered that genetic factors determined (1) whether the costa was excurrent or short and (2) whether the leaves were falcate or straight. Combinations of these two hereditary characters produce three varieties in *D. aduncus*: var. *typicus* with falcate leaves and a short costa; var. *Kneiffii* with straight leaves and a short costa; and var. *capillifolius* with falcate leaves and an excurrent costa. In *D. exannulatus* the leaves are always falcate but the length of the costa varies.

Therefore I have recognized var. *typicus* with a short costa and falcate leaves and var. *Rotae* with an excurrent costa and falcate leaves.

Other characters, such as cell size and leaf length, are influenced by the environment and may vary on the same plant. In *D. aduncus*, *D. fluitans*, and *D. exannulatus* two habitat phases result from this type of variation: (1) short leaves and broad, oblong-linear cells; and (2) long, flexuose, widely-spaced leaves and long-linear cells. These phases may be found on the same plant, and they may be produced on any of the varieties. Leaves on the lower, and submerged portion of the stem of any of these species may be the aquatic phase (2) while the upper, emergent part of the same stem may be either typical or short-celled (1). However, if the lower, submerged leaves have an excurrent costa, the upper ones will have an excurrent costa also, though the cells may be different. Therefore, since the costa is the constant character, it is apparent that the length of the costa is controlled by genetic factors, while the leaf and cell size are conditioned by environmental factors. Falcate leaves are an expression of hereditary factors, for, if the leaves are falcate in one part of the stem, they will be falcate throughout, even though submerged or subjected to other modifying environmental conditions.

Environmental conditions producing habitat forms in Drepanocladus. The same habitat conditions produce similar forms in *D. fluitans*, *D. exannulatus*, and *D. aduncus*.

Zastrow¹³ carried out controlled experiments on mosses and compared growth submerged and emergent under identical conditions of pH. She found that, in general, growth under water led to pinnate branching, longer leaves, longer leaf cells, larger and more numerous alar cells, widely spaced leaves, and a weaker costa. These modifications are produced by submerged plants of *D. aduncus*, *D. fluitans*, and *D. exannulatus*.

The short-celled variation often seen in *Drepanocladus* occurs most commonly on the emergent stems of plants growing in water. However, this form appears to be the result of recent flooding. Apparently the form is produced when the plant has more water available than is customary in its habitat. When the water supply is abundant and constant, all the leaves are similar and characteristic of submerged growth. When the water supply fluctuates, different forms are produced on the same plant under the different conditions; one of the forms produced under these conditions is invariably the short-celled phase of *D. aduncus*, *D. fluitans*, or *D. exannulatus*. Consequently, plants growing in deep lakes are entirely the submerged phase, whereas plants which grow in temporary ponds and pools and intermittent streams produce the short-celled variation on part of their stem.

¹³ Experimentelle Studien über die Anpassung von Wasser- und Sumpfmossen. Pfl.-Forsch. 17: 1-70. 1934.

Field studies around the Huron River, Washtenaw County, Michigan, indicated this type of environmental fluctuation first in 1940. On May 14, when the water level in a pond near the river was high, plants which had produced the short-celled leaves on the emergent stems were collected (Wynne 1701). In the summer (June 30) when the pond was stagnant and the water level stable, all the new growth was the aquatic phase (Wynne 1712). On August 30 collections again showed that short-celled leaves had been produced by a rise in the water level (Wynne 2072). Later (October 15) and until winter the conditions remained stable and all the leaves produced were of the aquatic type (Wynne 2230). Similar reactions were observed in Reese's Bog, Cheboygan County, Michigan. June 29, 1942, with much water in the bog, the leaves on the growing stems were short-celled (Wynne 2453). With less water (July 30) the plants were producing typical leaves (Wynne 2591).

The evidence obtained from these and many similar field observations was substantiated by large herbarium collections and extensive field notes from Quebec by H. Dupret. Many of Dupret's collections are in series from the same locale taken at different dates. When the response of each species to environmental changes was known, then each plant told its own history. By examining leaves from different parts of a stem of *Drepanocladus*, it is possible to tell approximately under what environmental conditions those leaves were produced. This knowledge made possible the interpretation of herbarium specimens and the elimination of environmental fluctuations from the formal nomenclature in the genus.

Statistical studies. In order to understand the variation in the genus *Drepanocladus*, statistical studies, as well as field studies, were made of the variable species. Measurements were made of all diagnostic features including serrulation, acumination, size, attachment, decurrency, and distance apart of the leaves; size of cells at base, alar region, margin, and apex of leaves. By plotting the results, it was easy to see whether the population fell naturally into one or several units. This information was useful in determining whether or not certain varieties were valid.

Figure 2 shows the statistical evidence that was used in determining the varieties in *D. revolvens* and *D. uncinatus*. All collections of *D. uncinatus* were examined and measured and the length of the leaf was plotted on a single histogram. Two populations were then apparent: one with leaves 2.0–4.0 mm. long and another with leaves 4.4–5.5 mm. long. Previous to this study several varieties, called *plumulosum*, *abbreviatum*, *plumosum*, *gracilescens*, and *gracillimum*, had been separated because of shorter leaves and a more delicate habit. When these simple statistical studies indicated that such a separation was artificial, a further, more careful examination of

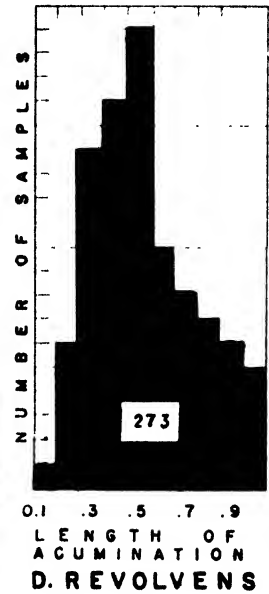
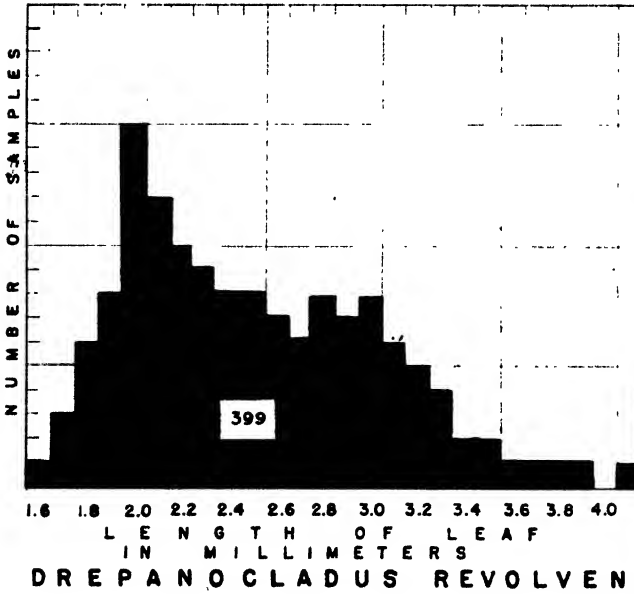
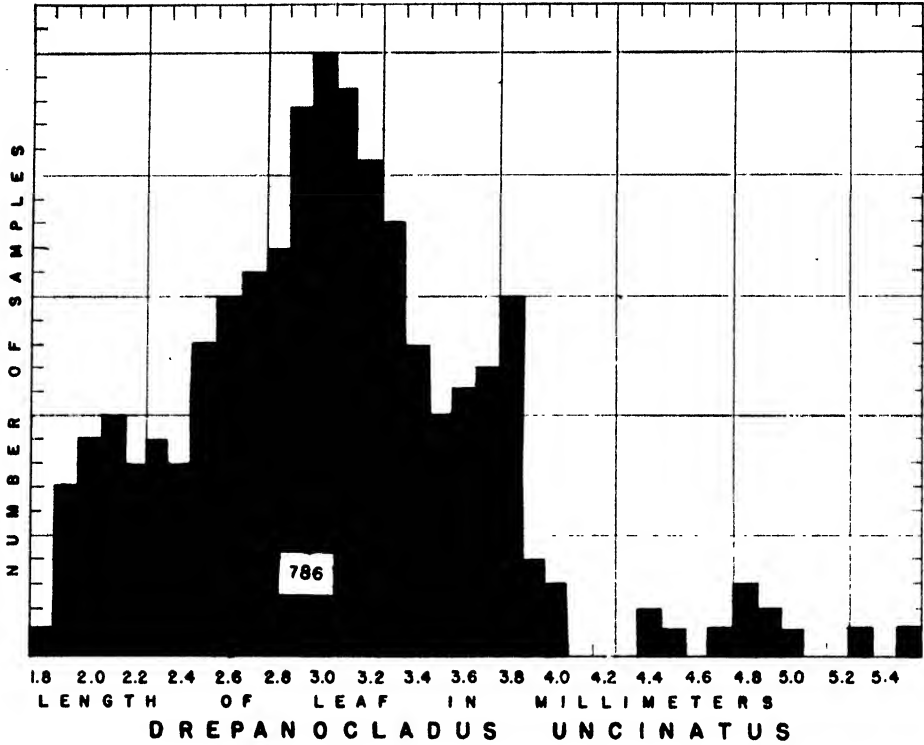


FIG. 2. Statistical data on *Drepanocladus uncinatus* and *D. revolvens*.

collections so named was made. In all these collections leaves of various lengths (2.2, 2.4, 2.5, 3.0, 3.2 mm.) were found in the same clone. The author believes, therefore, that small leaves are minor habitat variations of a large variable population, *D. uncinatus* var. *typicus*. The small group of plants with leaves 4.4–5.5 mm. long belong to *D. uncinatus* var. *subjulaceus*. The large size of the leaves on these plants is constant and correlated with a robust habit, a golden yellow color, and a distinct geographical range (western North America and Quebec and Newfoundland).

Length of leaf and length of acumination of plants known as *D. revolvens* and *D. intermedius* were measured and plotted on the same histogram. This indicated that *D. intermedius*, which had been separated from *D. revolvens* on the basis of its smaller leaves and shorter acumination, was not a natural population. Furthermore, examinations of many leaves from the same plant revealed acuminations varying in length from 0.1 to 0.8 mm. Therefore, on the basis of these observations, the name *D. intermedius* (Lindb.) Warnst. has been excluded and plants previously called *D. intermedius* placed in *D. revolvens*.

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STUDIES IN THE SIMAROUBACEAE—II. THE GENUS SIMAROUBA*

ARTHUR CRONQUIST

The genus *Simarouba* was founded in 1775 by Aublet, with *S. amara* Aubl. as the type species. Although it is frequently spelled *Simaruba*, the original spelling, *Simarouba*, must stand. *Simarouba* differs from the related *Quassia* L. and *Simaba* Aubl. in its unisexual flowers and long divergent stigmas, *Simaba* and *Quassia* having the flowers perfect and the single

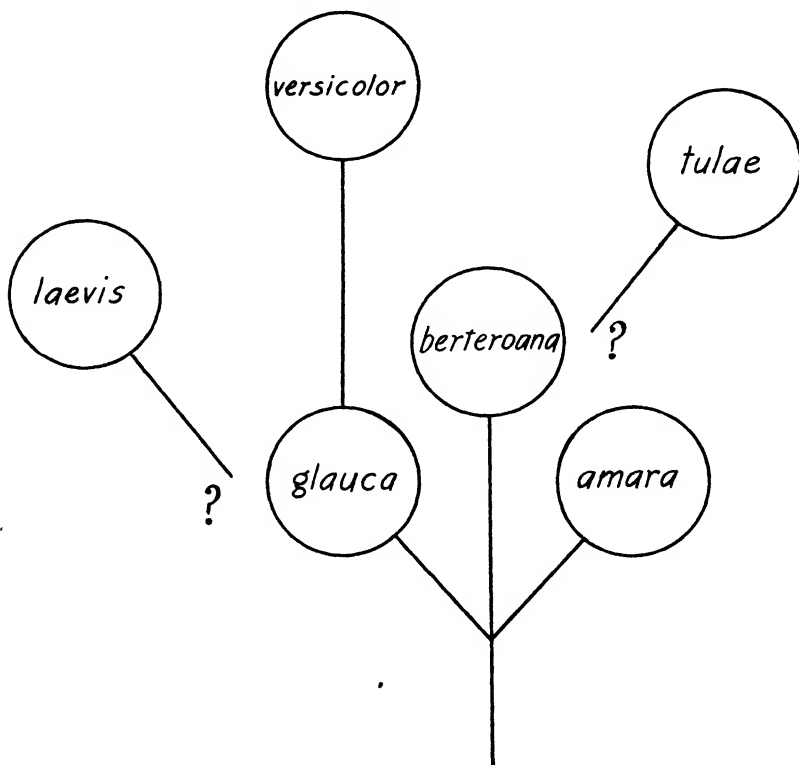


FIG. 1. Supposed phylogeny of *Simarouba*.

stigma capitate or slightly lobed. The gynophore in *Simaba* is usually larger and more conspicuous than in *Simarouba*, and the appendages of the filaments may be much longer, but these characters are not entirely dependable.

Although *Simarouba*, *Simaba*, *Quassia*, and the African *Odyndea* form

* The first paper of this series appeared in Jour. Arnold Arb. 25: 122-128. 1944.

an obvious and closely knit group, the origin of the group and the immediate derivation of the genus *Simarouba* are not clear. Within the genus, *S. amara*, *S. glauca*, and *S. Berteroana* are closely related and probably represent divergent end-lines of a common stock. *S. versicolor* is probably derived from *S. glauca*, or at least these two have a common ancestor more recent than the common ancestor of *S. glauca* and *S. amara*. *S. laevis* and *S. Tulae*, although clearly belonging to the genus, are each somewhat isolated, with obscure affinities. *S. Tulae* may be most closely related to *S. Berteroana*, while it might be hazarded that *S. laevis* is derived from *S. glauca*. These relationships are shown diagrammatically in figure 1.

Two sections have been proposed, *Porphyrosimarouba* for *S. Tulae*, and *Eusimarouba* for the rest of the species. If these are to be maintained, a third section should be set up for *S. laevis*, but the genus is so small that division into sections is of doubtful value, and I decline to establish any additional ones.

Nearly 500 herbarium sheets have been available for this study. I wish to thank Dr. H. A. Gleason and Mr. B. A. Krukoff, of the New York Botanical Garden, who have given continued advice and assistance, and Dr. R. T. Major, of Merck Research Laboratory, who has made this study possible. Also I wish to thank the curators of the several herbaria (hereinafter designated by the letters at the left), who have kindly loaned specimens:

- A—Arnold Arboretum, Harvard University, Jamaica Plain, Mass.,
- F—Field Museum, Chicago, Ill.,
- Mich—University of Michigan, Ann Arbor,
- MO—Missouri Botanical Garden, St. Louis,
- NY—New York Botanical Garden,
- US—United States National Herbarium, Washington, D. C.,
- Y—Yale University School of Forestry, New Haven, Conn.

Specimens cited as Kr. Herb. are mostly vouchers received by Mr. Krukoff in connection with samples for chemical study.

All measurements of flower parts are taken from specimens restored to normal size by boiling.

SIMAROUBA AUBL.

Trees or shrubs; leaves alternate, pinnately compound; leaflets 3–21, firm, offset or rarely some of them opposite; dioecious; inflorescence a complex mixed panicle, the staminate larger and with more numerous flowers than the pistillate; sepals 5, occasionally 4 or 6, united at the base; petals 5, occasionally 4 or 6, distinct; stamens appendaged at the base, 10, occasionally 8 or 12, in the pistillate flowers much reduced or absent; carpels 5, occasionally 4 or 6, borne on a short broad gynophore or disk, weakly united, with a short common style and divergent stigmas; the staminate flowers with the gynophore present but the carpels absent; ovules 1 in each carpel; fruit of several distinct drupes.

KEY TO SPECIES AND VARIETIES

1. Petals 9–11 mm. long; appendages of the filaments glabrous; leaflets elliptical, broadest near the middle; plant of Puerto Rico.....6. *S. Tulae*.

1. Petals 3.5–7 mm. long; appendages of the filaments with at least a few hairs at the tip, often densely hairy; leaflets either oblong, with parallel sides, or somewhat obovate and broadest above the middle, except sometimes in *S. Berteroana*; plants of South and Central America, Florida (U. S. A.), and the West Indies, but not of Puerto Rico.

2. Leaflets mostly 3–5, sometimes 7, not at all veiny beneath; gynophore of the staminate flowers very short, the filaments inserted essentially at the edge of its top, distinctly not inferior to it; petals about 4.5–5.5 mm. long; anthers about 1.2–1.4 mm. long; plant of Cuba.....5. *S. laevis*.

2. Leaflets mostly 9 or more, sometimes only 7, in *S. Berteroana*, with evident veins beneath except in forms of *S. amara*; gynophore of the staminate flowers relatively well developed, the filaments inserted distinctly below it; plants of general distribution, including Cuba.

3. Appendages of the filaments densely hairy, relatively short and broad, the attached portion no longer than the free portion; free portion of the appendages bent over and closely investing the gynophore, in the staminate flowers; leaflets from minutely rugulose and dull to papillate and glaucous beneath.

4. Petals 4.5–7 mm. long; anthers 1.2–2.0 mm. long; venation various; plants of Haiti, the Dominican Republic, Jamaica, Cuba, the Bahamas, Florida (U. S. A.), southern Mexico, and Central America.

5. Leaflets glaucous beneath, the surface closely papillate; main veins evident as distinct dark lines on the lower surface; leaflets tending to be obtuse or rounded at the apex; anthers 1.5–2.0 mm. long, or sometimes only 1.3 mm. in var. *typica*; plant of Cuba, Jamaica, the Bahamas, southern Florida, southern Mexico, and Central America, as well as occasionally Haiti and the Dominican Republic.3. *S. glauca*.

6. Leaflets relatively narrow, mostly more than 3 times as long as wide, except for some of the basal ones; plant of Cuba and occasionally Jamaica.3A. *S. glauca* var. *typica*.

6. Leaflets relatively broad, mostly at least $\frac{1}{2}$ as wide as long; range of the species, but uncommon in Cuba.

3B. *S. glauca* var. *latifolia*.

5. Leaflets not glaucous beneath, the lower surface minutely rugulose and punctate, or very minutely papillate; leaflets tending to be abruptly acute at the tip; main veins discernible as faint furrows or as light lines on the lower surface; anthers mostly 1.2–1.4 mm. long; plant of Haiti and the Dominican Republic.2. *S. Berteroana*.

4. Petals 3.5–4.5 mm. long; anthers 0.7–1.0 mm. long; veins on the lower surface of the leaflets obscure or visible as furrows; plant of South and Central America, and the West Indies as far north as Antigua.1. *S. amara*.

5. Leaflets glaucous beneath, the surface papillate.

1B. *S. amara* var. *opaca*.

5. Leaflets not glaucous beneath, the surface minutely rugulose and punctate, or very minutely papillate.1A. *S. amara* var. *typica*.

3. Appendages of the filaments sparsely to sometimes rather densely hairy, relatively long and narrow, the attached portion longer than the short free portion; free portion of the appendages somewhat raised above the gynophore, not closely investing it, in the staminate flowers; petals about 4.5–5.5 mm. long; anthers 1.0–1.4 mm. long; lower surface of the leaflets glaucous, bearing a minute close reticulum of waxy material, the occasional larger than the average

areolae giving a somewhat punctulate appearance under low magnification (often densely hairy, and the reticulum thus obscure).

4. *S. versicolor*.

4. Leaflets conspicuously hairy beneath.4A. *S. versicolor* var. *typica*.

4. Leaflets glabrous or nearly so beneath.4B. *S. versicolor* var. *pallida*.

SYSTEMATIC TREATMENT OF THE SPECIES

1. SIMAROUBA AMARA Aubl. Pl. Gui. 2: 860. pl. 331, 332. 1775.

Tree 7–35 meters high; leaflets mostly 9–21, elliptic-oblong, usually broadly so, with nearly parallel sides, cuneate at the base, rounded to sometimes abruptly short-acuminate at the apex, mostly 6–15 cm. long, 2–6 cm. wide, the lowermost ones sometimes smaller, glabrous, the lower surface dull and rugulose to papillate-glaucous, the veins obscure or showing as furrows; calyx about 1 mm. long or a little more, glabrous or finely puberulent, the broad teeth equaling or shorter than the tube, petals 3.5–4.5 mm. long, green, yellow-green, or sometimes white, appendages of the filaments densely hairy, relatively short and broad, the attached portion no longer than the free portion, which bends over and closely invests the gynophore, in the staminate flowers; anthers 0.7–1.0 mm. long; fruit about 1–1.5 cm. long, ellipsoid, 2-ridged.

1A. SIMAROUBA AMARA Aubl. var. *typica* Cronquist, var. nov.

S. amara Aubl. Pl. Gui. 2: 860. Pl. 331, 332. 1775.

Quassia Simarouba L.f. Suppl. 234. 1781.

Zwingera amara Willd. Sp. Pl. 2: 569. 1799.

Lower surface of the leaflets minutely rugulose and punctate, or very minutely papillate, dull.

Type: *Aublet s. n.*, French Guiana.

Distribution: Brazil, Bolivia, and Peru, north to Costa Rica, in Central America, and Antigua, in the West Indies.

ANTIGUA¹: *Box* 1415 (US). MONTSEERAT: *Shafer* 365 (=565), (NY). GUADELOUPE: *Duss* 2973 (MO), 3427 (F, NY, US); *Stehle* 2587 (US). MARTINIQUE: *Duss* 1198 (NY); *Hahn* 145 (US). DOMINICA: *Cooper* 161 (Mich, US); *Fishlock* 38 (MO, NY, US). BARBADOS: *Eggers* 7150 (A, US); *Stehle* 2982 (NY). GRENADA: *Broadway s. n.*, May 1, 1906 (F, MO, NY). TRINIDAD: *Brooks s. n.* (Kr. Herb. # 16137). BRITISH GUIANA: *Wood s. n.* (Kr. Herb. # 16167). Essequibo: *Smith* 2857 (A, MO, NY, US). DUTCH GUIANA: *Stahel s. n.* (Kr. Herb. # 16245). FRENCH GUIANA: *Melinon s. n.* (year 1863) (A). BRAZIL: *Glaziov* 17234 (NY). Amazonas: *Ducke* 374 (Kr. Herb., Y). Basin of Rio Madeira: *Krukoff* 6314 (A, NY, US), 7198 (A, MO, NY, US). Basin of Rio Negro: *Ducke* 60 (A, F, MO, NY, US). Basin of Rio Purus: *Krukoff* 5240 (A, MO, NY, US). Basin of Rio Solimoes: *Krukoff* 8176 (A, MO, NY). Para: *Capucho* 470 (F); *Carr* 326 (F); *Moss* 56 (US). Maranhao: *Froes* 32 (US), 1966 (A, MO, NY, US), 11910 (A, NY). Ceara: *Luetzelburg* 26343 (F). Bahia: *Curran* 11 (US, Y), 21 (Y); *Froes* 69 (Kr. Herb.), 97 (Kr. Herb.); *Froes s. n.* (Kr. Herb. # 16715). Matto Grosso: *Krukoff* 1462 (A, NY). Minas Geraes: *Barreto* 1258 (F). BOLIVIA: La Paz: *Krukoff* 10524 (A, MO, NY), 11019 (A, MO, NY). PERU: *Tessman* 5431

¹In view of the potential economic importance of *Simarouba amara* and *S. glauca*, it has been thought desirable to cite all specimens examined. This has been done at the expense of the Research Department of Merck & Co., Inc.

(NY). San Martin: *Klug 3741* (A, MO, NY, US). Loreto: *Klug 323* (F, NY, US), *639* (F, NY, US), *3207* (A, F, MO, NY, US). CANAL ZONE: *Carpenter 42* (F); *Starry 144* (F). COSTA RICA: San Jose: *Skutch 2510* (A, Mich, MO, NY, US), *4032* (A, MO, NY). Limon: *Standley & Valerio 48428* (US).

1B. SIMAROUBA AMARA Aubl. var. OPACA Engl. Nat. Pfl. 3(4): 213. 1896.

S. opaca Radkl. ex Engl. Nat. Pfl. ed. 2 19a: 374. 1931.

Lower surface of the leaflets papillate, glaucous.

Type: "in Nordbrasilien (Para, Alto Amazonas) und Bahia, auch cultiviert bei Rio de Janeiro."

Distribution: Brazil to British Honduras; apparently absent from the West Indies.

GUATEMALA: El Peten: *Cook & Martin 75* (US). Jutiapa: *Standley 75955* (F). BRITISH HONDURAS: *Hope 1* (F, Y); *Gentle 1870* (A, F, Mich, NY), *2751* (A, Mich, NY), *3280* (A, Mich, MO, NY); *Schipp 123* (F, MO, NY, US); *Stevenson s. n.* (Kr. Herb. # 16180). HONDURAS: Atlantida: *Standley 52807* (A, US), *55546* (A, US). EL SALVADOR: La Union: *Beetle 26257* (A, MO). VENEZUELA: *Tate 1152* (NY). Bolivar: *L. Williams 11774* (F, Kr. Herb., US). BRITISH GUIANA: Mount Roraima: *Tate 241* (NY). BRAZIL: Amazonas: Basin of Rio Branco: *Kuhlmann 3038* (US). Pasin of Rio Negro: *Krukoff 7932* (A, MO, NY). Para: *Spruce 442* (NY). Bahia: *Blanchet 2727* (MO, NY); *Curran 98* (US); *da Cunha s. n.* (Kr. Herb. # 16483).

Simarouba amara has long been confused with *S. glauca*, but the two are amply distinct. The differences in size of anthers and petals are of critical importance. The petals in *S. amara* are dull yellow-green, or sometimes whitish, while those of *S. glauca* are commonly brighter yellow, not infrequently with a touch of orange or red. *S. amara* is a large tree of the rain-forest; *S. glauca* is commonly a large shrub or small tree, often of somewhat drier and more open habitats. The key difference in leaf venation is not entirely constant; individuals having leaves seemingly intermediate between *S. glauca* and *S. amara* var. *opaca* are clearly referable to *S. glauca* on the basis of flower structure.

2. SIMAROUBA BERTEROANA Krug & Urb. Bot. Jahrb. 15: 306. 1892.

Tree; leaflets mostly 7-9, relatively widely spaced, glabrous, cuneate and usually slightly oblique at the base, usually abruptly short-pointed at the apex, narrowly elliptic to broadly elliptic-ovate, about 5-10 cm. long, 1.5-3.5 cm. wide, the lower surface dull and minutely rugulose, very minutely papillate, the veins showing as faint furrows or sometimes more evident lines; calyx a little over 1 mm. long, sometimes pruinose-glaucous, the broad rounded lobes equaling or exceeding the tube and sometimes finely ciliate on the margins; petals yellow-green, about 4.5-6 mm. long; appendages of the filaments like those of *S. amara* and *S. glauca*; anthers about 1.2-1.4 mm. long; fruit about 1.5-2 cm. long, 2-ridged.

Type: *Bertero 64*, Dominican Republic (NY—fragment and photo).

Distribution: Haiti and the Dominican Republic.

HAITI: *Desert s. n.* (Y); *Ekman H3036* (US); *Leonard 4265* (NY, US). DOMINICAN REPUBLIC: *Fuertes 47* (F, MO, NY, US); *Jimenez s. n.* (Kr. Herb. # 16334); *Schiffino 92* (US, Y).

This species combines the characters of *S. amara* and *S. glauca*, but seems genetically stable. In leaf texture and venation it resembles *S. amara*; in petal size it simulates *S. glauca*. The anthers are larger than in *S. amara*, and about at the lower size limit for *S. glauca*. The pronounced tendency toward abruptly acute leaflets, a feature found only occasionally in *S. amara*, and scarcely at all in *S. glauca*, suggests that it is a residual stock rather than a stabilized hybrid.

3. SIMAROUBA GLAUCA DC. Ann. Mus. Paris 17: 424. 1811.

Large shrub, or small tree, rarely larger and as much as 18 meters high; leaflets mostly 8–16, cuneate at the base, rounded to occasionally acutish at the apex, narrowly obovate to broadly elliptic-oblong, mostly 4–10 cm. long, 12–50 mm. wide, the lowermost ones sometimes smaller; lower surfaces of the leaflets glabrous to sometimes moderately appressed-hairy, conspicuously papillate-glaucous and evidently reticulate-veiny, the veins appearing dark in herbarium specimens; calyx a little over 1 mm. long, glabrous, often also somewhat pruinose-glaucous, the broad rounded lobes equaling or exceeding the tube, sometimes finely ciliolate on the margins; petals 4.5–7 mm. long, mostly yellow-green, sometimes brighter yellow and with an orange-red midstripe; appendages of the filaments much like those of *S. amara*; anthers 1.5–2.0 mm. long, or sometimes only 1.3 mm. long in var. *typica*; fruit about 1.5–2.0 cm. long, ellipsoid, 2-ridged.

3A. SIMAROUBA GLAUCA DC. var. *typica* Cronquist, var. nov.

S. glauca DC. Ann. Mus. Paris 17:424. 1811.

Quassia glauca Spreng. Syst. 2:319. 1825.

Leaflets narrower in shape and averaging smaller than those of var. *latifolia*, mostly more than three times as long as wide, except sometimes some of the basal ones; anthers sometimes a little smaller than in var. *latifolia*.

Type: Humboldt & Bonpland s. n., near Havana, Cuba.

Distribution: Cuba, and apparently occasionally in Jamaica.

CUBA: Gill & Whitford s. n. (year 1925) (Y); Leon 2597 (NY); Rugel 209 (NY). Pinar del Rio: Britton & Cowell 9915 (NY). Isla de Pinos: Britton, Wilson & Leon 15271 (NY). Matanzas: Britton & Wilson 14048 (NY, US). Santa Clara: Acuna s. n. (Kr. Herb. # 16053); Britton, Britton, & Wilson 5570 (NY, US); Britton, Cowell, & Earle 10304 (NY); Britton, Earle, & Wilson 4624 (NY, US); Britton & Wilson 5534 (NY, US), 5658 (NY); Jack 4194 (A, NY), 4511 (A), 4834 (A, NY); Rehder 1112 (A), 1213 (A); Shafer 12312 (NY, US). Camaguey: Shafer 318 (NY, US), 1086 (NY, US). JAMAICA: Harris 9551 (NY).

3B. SIMAROUBA GLAUCA DC. var. *latifolia* Cronquist, var. nov.

S. officinalis DC. Ann. Mus. Paris 17:423. 1811, in part.

S. medicinalis Endl. Med.-Pfl. Osterreich. 528. 1842.

S. officinalis DC. forma *glabra* Krug & Urb. Bot. Jahrb. 15:305. 1892.

Leaflets broader and averaging larger than those of var. *typica*, mostly at least 1/3 as wide as long.

A var. typico differt foliis latioribus, latitudine saltem tertiam partem longitudinis aequanti.

Type: Curtiss 5625, Key West, Florida, April 18, 1896 (NY); isotypes at MO, US.

Distribution: Central America (Costa Rica) to Mexico (Oaxaca); southern Florida (U.S.A.); Bahama Islands; Jamaica; occasional in Cuba, Haiti, and the Dominican Republic.

MEXICO: *Rovirosa* 730 (US). Oaxaca: *L. Williams* 9375 (F). Tabasco: *Matuda* 3116 (A, F, Mich, NY). Yucatan: *Gaumer* 439 (A, F, MO, NY, US), 23252 (A, MO, NY, US), 23583 (F, MO, US), 24111 (F, MO, US). BRITISH HONDURAS: *Brown* 33 (F, Y); *Carnegie Institute & U. of Michigan 3rd Biological Exp.* 4350 (F, Mich); *Gentle* 381 (F, Mich, US), 417 (A, F, Mich, MO, US), 1200 (A, Mich, MO, NY, US); *Heyder* 8 (US, Y); *Lundell* 4350 (F); *Turner s. n.* (Kr. Herb. # 16301). GUATEMALA: *Deam* 195 (A, Mich); *Friedrichsthal* 923 (F); *Record & Kuylen* G128 (US, Y). El Peten: *Bartlett* 12662 (A, Mich, NY, US); *Lundell* 2185 (A, F, Mich, US). 2234 (A, F, Mich, US); *Mercedes* 363 (Mich). Baja Verapaz: *Cook & Doyle* 92 (US); *Kellerman* 6634 (F). Izabal: *Kellerman* 4512 (F, US); *Steyermark* 38125 (F). El Progreso: *Popenoe* 982 (US). Zacapa: *Standley* 72030 (F); *Steyermark* 29303 (F). Jalapa: *Kellerman* 7004 (F), 7896 (F, NY). Amatitlan: *Morales* 738 (US). Jutiapa: *Standley* 60550 (F). HONDURAS: Camayagua: *Edwards* 91 (A, F), 373 (A, F, US), 571 (A, F, US). Yoro: *Standley* 55047 (A, US). EL SALVADOR: *Villacorta* 8136 (US). La Libertad: *Standley* 23222 (US). San Salvador: *Calderon* 257 (NY, US); *Renson* 233 (NY, US). San Vicente: *Standley* 21232 (US). La Union: *Standley* 20692 (NY, US). NICARAGUA: Leon: *Baker* 2266 (A, MO, NY, US). Managua: *Chavez* 173 (US); *Garnier* 3009 (A). Masaya: *Mazon* 7674 (US). COSTA RICA: Puntarenas: *Quiros-Calvo* 798 (F). UNITED STATES: Florida: *Bessey* 20 (A); *Blodgett s. n.* (NY); *Curtiss* 439 (Mich, MO, NY, US), 5625 (MO, NY, US), *s. n.* (March, 1882) (A); *Duckett* 218 (A, NY, US); *Farnum s. n.* (February, 1930) (Mich, MO, US); *Fennell* 329 (A, NY), *Garber s. n.* (year 1877) (MO, US); *J. A. Harris* C21345 (US); *A. H. Howell* 875 (US); *MacDonald* 34 (Y); *Moldenke* 823 (MO, NY, US), 3669 (NY); *Mosier* 379 (US); *O'Neill* 7585 (A, NY, US), *s. n.* (August 21, 1929) (MO, US); *Pollard, Collins, & Morris* 187 (NY, US); *Rehder* 713 (A); *Rugel* 107 (MO, US), 108 (NY, US); *Safford & Mosier* 89 (US), 90 (US); *Sargent s. n.* (April 6, 1886) (A), (April 13, 1886) (A), (April 20, 1886) (A); *Simpson* 346 (US), 564 (NY), 564a (US); *Small* 7451 (NY, US), 8766 (NY), 8842 (NY); *Small, Mosier, & Small* 6428 (NY); *Small & Nash* 16 (NY); *Small & Small* 4712 (MO, NY). BAHAMA ISLANDS: *Brace* 1648 (NY), 3913 (NY), 6795 (NY); *Britton & Millspaugh* 2649 (NY); *Small & Carter* 8725 (NY, US). CUBA: Oriente: *Britton & Cowell* 12533 (NY, US). Santa Clara: *Jack* 4565 (cultivated) (A, US), 5103 (cultivated) (A, US). DOMINICAN REPUBLIC: *Valeur* 845 (MO, NY); *Wright, Parry, & Brummel* 174 (F, US). HAITI: *Cook* 12 (US). JAMAICA: *R. C. Alexander s. n.* (year 1850) (MO, NY); *Britton* 3767 (NY); *Harris* 5931 (NY), 8664 (NY, US), 9358 (A, NY); *Hart* 1053 (F, US), *s. n.* (US).

Some of the Central American plants (exemplified by *Edwards* 571, Camayagua, Honduras) have conspicuously longer (up to 7 mm.) and more brightly colored petals than usual, and the *Edwards* plant is reported to be a tree 60 feet high; without additional material it is difficult to say whether these represent a true variety or merely an unusual form.

S. officinalis DC. was based on at least two elements; most of the specimens cited would seem to belong to a slightly pubescent phase of *S. glauca* var. *latifolia*, but the extensive synonymy given all refers to *S. amara*.

4. SIMAROUBA VERSICOLOR A. St. Hil. Pl. Us. Bras. pl. 5. 1824.

Small tree mostly 4-5 meters high; leaflets mostly 9-16, narrowly obovate to broadly oblong or elliptic-oblong, cuneate at the base, rounded to acutish at the tip, mostly 4-10 cm. long and 1.5-3.5 cm. wide, the lowermost ones sometimes smaller, the lower surface provided with a minute close waxy reticulum that is ordinarily readily visible under a magnification of 25 diameters (unless obscured by pubescence), the occasional larger than average areolae often giving a minutely punctulate appearance under low magnification, the surface varying from otherwise glabrous to densely spreading-hairy; calyx about 1 mm. long or a little more, glabrous or sparsely hirtellous, the broad rounded lobes about as long as the tube, often ciliolate on the margins; petals about 4.0-5.5 mm. long; appendages of the filaments sparsely to sometimes rather densely hairy, relatively long and narrow, the attached portion longer than the short free portion, which is raised somewhat above the gynophore, in the staminate flowers, instead of closely investing it; anthers about 1.0-1.4 mm. long; fruit about 2-2.5 cm. long, ellipsoid or ovoid, 2-ridged.

4A. SIMAROUBA VERSICOLOR A. St. Hil. var. *typica* Cronquist, var. nov.

S. versicolor A. St. Hil. Pl. Us. Bras. pl. 5. 1824.

S. versicolor A. St. Hil. var. *angustifolia* Engl. in Mart. Fl. Bras. 12(2): 226. 1874.

Lower surface of the leaflets more or less densely spreading-hairy.

Type: "Dans les paturages de la province de Minas Geraes, voisins du Rio-de-S.-Francisco," Brazil.

Distribution: Semi-open places; eastern Brazil, from Maranhao to Minas Geraes, thence westward to Bolivia.

BRAZIL: *Herb. Drake s. n.* (F); *Glaziov s. n.* (A). Ceara: *Gardner 1513* (NY, US); *Luetzelburg 25828* (F). Bahia: *Blanchet 3142* (NY); *Luetzelburg 1456* (NY). Maranhao: *Smethelegg 723* (US). Matto Grosso: *Malme 1537* (US); *Martius Herb. 572* (MO, NY). Rio de Janeiro: *Glaziov 10463* (US). BOLIVIA: *Kuntze s. n.* (July, 1892) (NY).

4B. SIMAROUBA VERSICOLOR A. St. Hil. var. *pallida* Engl. in Mart. Fl. Bras. 12(2): 226. 1874.

Lower surface of the leaflets glabrous.

Type: "In prov. Goyaz inter arbuscula tortuosa pr. Paracaitu, et in Chapado de S. Marcos prov. Minas Geraes," Brazil.

Distribution: Semi-open places; eastern Brazil, from Ceara and Piauhy to Minas Geraes, thence westward to Bolivia.

BRAZIL: *Pohl 935* (F) Ceara: *Ule 9044* (US). Piauhy: *Dahlgren 981* (F). BOLIVIA: El Beni: *Rusby 1361* (NY), *1714* (NY, US). Santa Cruz: *Steinbach 6410* (F), *7210* (F, MO, NY), *7269* (F, MO, NY).

The peculiar waxy reticulum on the lower surface of the leaflets is quite enough to identify either variety of this species, even in the absence of flowers. From the available specimens it would seem that var. *typica* is more common in Brazil, while var. *pallida* is more common in Bolivia. No specimens have been found to connect definitely the Brazilian with the Bolivian range, but such a connection doubtless exists.

5. *SIMAROUBA LAEVIS* Griseb. Cat. Pl. Cub. 49. 1866.

Shrub or small tree, mostly 2-6 meters high; leaflets mostly 3-5, sometimes 7, glabrous, obovate or elliptic, cuneate at the base, rounded at the summit, 3-7 cm. long, 1.5-3 cm. wide, the lower surface dull, minutely rugulose and punctulate, not at all veiny, or very obscurely so; calyx about 1.5 mm. long or a little more, glabrous except sometimes for some ciliae on the margins of the broad rounded lobes, which slightly exceed the tube; petals about 4.5-5.5 mm. long, reported to be white; filaments inserted essentially at the edge of the top of the very short gynophore, in the staminate flowers; appendages thick, firm, erect, the free portion longer than the short attached portion; anthers about 1.2-1.4 mm. long; fruit about 1.5-2 cm. long, ellipsoid, 2-ridged.

Type: Wright 2187, eastern Cuba (MO, NY, fragments).

Distribution: Cuba.

CUBA: Britton, Britton, & Shafer 703 (NY). Pinar del Rio: Leon & Roig 13542 (NY). Habana: Leon 2931 (NY), 5204 (NY); Leon & Cesaere 8938 (NY). Matanzas: Britton, Britton, & Wilson 14068 (NY, US). Santa Clara: Britton, Britton, & Wilson 6204 (NY); Britton & Cowell 10194 (NY), 13282 (NY); Jack 5417 (A). Oriente: Wright 1159 (NY).

6. *SIMAROUBA TULAE* Urb. Jahrb. Bot. Gart. Berlin 14: 245. 1886.

Shrub or tree, mostly 2-8 meters high; leaflets mostly 5-10, offset or sometimes some of them opposite, glabrous, cuneate at the base, abruptly acuminate at the apex, elliptic, broadest about the middle, 5-11 cm. long, 1.5-5 cm. wide, dull, very minutely papillate, and often somewhat brownish, on the lower surfaces; inflorescence relatively broad and short; calyx about 1.5 mm. long or more, glabrous, the broad obtuse or rounded lobes equaling or exceeding the tube, petals about 9-11 mm. long, red; appendages of the filaments relatively long and slender, glabrous, the attached portion longer than the short free portion; anthers about 1.5 mm. long, or a little more; fruit, strongly flattened, broadly and asymmetrically obovate, 2-3.5 cm. long, red.

Type: Wydler 418, *prope* Maricao, Puerto Rico.

Distribution: Puerto Rico.

PUERTO RICO: Britton & Cowell 4221 (NY, US); Britton, Cowell, & Brown 4452 (MO, NY, US); Britton & Marble 679 (NY, US); Britton, Stevens, & Hess 2463 (NY, US); Eggers 1284 (US); Gregory 54 (NY); Hess 1461 (NY), 2208 (NY); Hioram s. n. (July, 1931) (NY); Holdridge 224 (NY); McClelland 9134 (NY); Sargent 605 (US); Sintensis 277 (US), 297 (US), 1329 (US), 2550 (US), 4392 (US), 4683 (F, MO, NY, US).

EXCLUDED SPECIES

Simarouba excelsa DC. Ann. Mus. Par. 17: 424. 1811. = *Picrasma excelsa* (Sw.) Planch.

Simarouba monophylla Oliver Ic. Pl. pl. 1387. 1882. = *Simaba* sp.

Simarouba obovata (Spruce ex Engl.) Engl. Nat. Pf. 3(4): 212. 1896. = *Simaba obovata* Spruce ex Engl.

THE NEW YORK BOTANICAL GARDEN
NEW YORK

SOME STATISTICS OF *ACHRAS ZAPOTA* LEAVES, BRITISH HONDURAS¹

FRANK E. EGLER

PURPOSE OF THE STUDY

The taxonomic status of the *Achras* complex in Central America is still in need of further investigation. Of this complex *Achras zapota* is the most commonly recognized species.² This tree is the source of the chicle of commerce, which is used as a base for chewing gum and is derived from the coagulation of the latex of the bark. The gathering of the latex by professional chicleros is an industry of considerable local importance. *Achras zapota* also produces the fruit known as sapodilla, found in local markets in many parts of the tropics. The wood of *Achras* is generally recognized as being durable, and it is claimed that certain beams in Mayan ruins, probably 1000 to 1500 years old, are still sound. Furthermore, *Achras* is a forest tree of considerable importance in the local vegetation, both because of its numbers and its size. For these reasons, the recognition of species, strains and types is a matter of practical and academic significance.

Both the existing literature on the *Achras* complex and treatments of the genus in regional manuals and local native opinion emphasize the importance of leaf shape in the segregation of taxonomic entities. Furthermore, differences in normal leaves of the sapodilla are such that their taxonomic significance deserves further investigation. The purpose of this paper is to present certain statistics on normal leaf variation in a population of *Achras zapota*, as an impartial contribution to our knowledge of that segregate. Such statistics may serve as a base for evaluation of botanical collections made elsewhere. Data on floral variation and evaluation of floral variation are not here considered.

¹ Contribution No. 1 from the Chicle Development Company Experiment Station. Professor C. C. Carpenter, Syracuse University, has reviewed the use of statistical methods in this study. Comments on the manuscript have been received from Professors R. R. Hirt, J. L. Lowe, H. F. A. Meier, and H. K. Phinney, N. Y. State College of Forestry, and from Professor Stanley A. Cain, University of Tennessee.

² Gilly (Trop. Woods 73: 1-22. 1943), has shown that the name *Achras zapota* is untenable, and has proposed *Manilkara zapotilla* (Jacq.) Gilly to replace it. He has split *Achras zapota* into ten species, primarily on the basis of floral characters, of which species nine are new. Because the present author is not yet in the position to recognize these additional species, because Gilly himself writes that his "paper must be regarded as only a preliminary step toward the solution of the Sapodilla-Nispero complex," and because the old name is firmly entrenched in the practical literature, he is retaining the established binomial pending further investigations.

An additional purpose of this study is to test for significant leaf differences between the so-called "color varieties" of *Achras zapota*. These color varieties, the *blanco* (white), the *colorado* (red), and the *morado* (blue) are generally distinguished without hesitation by native chicleiros. The distinctions, however, are obscure and inconstant to botanists. Nevertheless it seems to be a scientific practice to place faith in a tropical native's ability to separate species, a situation sometimes carried to such extremes as would not be accepted in north temperate regions. The very seriousness with which the situation is being accepted for *Achras* makes a report of this kind desirable.

On the basis of the literature and the author's studies in the Yucatan peninsula, it would appear that identification of a color variety represents a chicleiro's *opinion* on the latex yield of the tree if it were to be tapped. Since commercial tapping is unsupervised, there is no check on a chicleiro's determination, although past studies by the Chicle Development Company indicate that his opinion is not to be taken seriously. The basis of recognition of the varieties is variously reported in the literature, and differs according to region and the individual chicleiro. Leaf features are mentioned repeatedly, as well as external bark, color of internal bark, site, form of tree, number of previous tappings, and type of fruit. The author has found different chicleiros to give different determinations for the same tree, and has found a chicleiro to change his determination on closer inspection of a tree. A test machete cut, permitting flow of latex, convinces the chicleiro, but not the botanist, as to whether it is a low-yielding red, a high-yielding white, or a very high-yielding blue.

The chicle industry has long recognized that trees differ extremely in the quantity of latex they will yield. It takes no mystic or unusual perspicacity on the part of a field botanist to observe certain correlations between site and morphologic features of the trees. Trees of thin rocky soil and of seasonally parched "akalches" are small, short-boled, open-crowned, limby, exposed to wind, light, and dryness, with deeply fissured bark, and a small amount of latex-yielding inner bark. Trees of deep soil are large, long-boled, close-crowned, in a dense moist shady forest, with shallowly fissured bark, and a greater amount of inner bark. The xeric form is usually the chicleiro's *colorado*, the hygric form is usually the *blanco*.

FIELD METHODS

The field investigations were carried out in April, 1942, on the Tower Hill East Estate, a unit of the Honey Camp Experimental Forest of the Chicle Development Company Experiment Station in northern British Honduras. The property belongs to the Chicle Development Company of New York, Central American subsidiary of the Beech-Nut Packing Co. and the American Chicle Co. The Tower Hill East Estate was originally purchased

as a typical example of British Honduras sapodilla forest. For statistical purposes one may consider that any other sample of such forest had an equal chance of serving for this study.

The populations sampled were along two arbitrarily chosen foot trails, one in general upland, the other in akalche. The course of the trails bore no relation to local topography, and it may be considered that all trees in the Estate had equal chances of occurring along them.

Thirty-five permanently located trees were used in this study, chosen for purposes of comparing the color varieties, and with as much adherence to the principles of random sampling as the peculiar conditions permitted. Four assumedly homogeneous populations were considered: Upland White, Upland Red, Upland Blue, and Akalche Red. No white or blue trees were found in akalche. For each population, the first 10 trees occurring on the line of travel were accepted (except that only 5 of the rare blues were found). About 6 trees were passed which were difficult or dangerous to climb because of luxuriant lianas or of decay resulting from severe tappings, both of which characteristics were assumed to have no correlation with possible botanical differences. Recognition of the color varieties was by an unusually competent and intelligent chichero.

From each of the 35 trees, foliage was obtained from approximately midheight of the crown, cut by a chichero in the presence of the author. Specified location within the crown may have been unnecessary, since it appeared by observation that there was no apparent difference between the types of foliage growing in different parts. The entire crown of *Achras* is open, limby, usually rising above the surrounding vegetation, and well exposed to light in all its parts.

From 1 to 5 small branches were cut by the chichero, and from them material for herbarium specimens was taken. It is characteristic of *Achras zapota* that the foliage is grouped at the ends of twigs in spreading rosettes (forming a pattern against the sky that aids in field identification), and 10 such rosettes were chosen at random from each tree. In conformity with the plan of this study for sampling only the normal foliage, certain dwarfed, curled, diseased, or abnormally large rosettes were discarded. Every investigator who has carefully observed the full variation of leaves on any one tree realizes that although close to 100 per cent of the foliage forms an intergrading mass, there are certain extremes—as would be midgets and giants in a human population—which can be eliminated in all except very large sampling techniques, here impractical. These leaf abnormalities appeared consistently in all trees, and did not differentiate the trees. Furthermore, the elimination of this small percentage from the analysis affected only the extreme range, a statistic which has not been considered of botanical importance. As a general observation, it may be said that there was sometimes an

obvious individuality of leaf type on a single tree. Such apparent individuality was not carried over to any second tree or group of trees, and careful observation of the foliage of additional trees made it appear that it was nothing more than one phase of varying conditions. The leaf features for statistical treatment, however, were chosen with this individuality in mind.

Rosettes both with new light green foliage and with old dark green foliage were taken. At this season, the early part of the dry season, fall of old leaves and growth of new leaves had been so rapid that approximately three-quarters of the trees showed only new foliage (the light color of which is another aid in field identification). It was determined by observation of rosettes with leaves of both ages that the new set had already attained their full areal growth, and consequently the classes have not been segregated in this study. The young thin leaves are sometimes larger than the old thick leaves, and it is possible that there is a small seasonal variation, with the larger leaves being formed in the period of most rapid growth.

After being dried as herbarium material, and after the leaves had regained enough moisture from the atmosphere that they were no longer brittle, 2 leaves were selected from each rosette for detailed study. Although there was generally only minor variation in size within a rosette, leaves of medium length were deliberately chosen, in accordance with the plan to characterize variations in normal foliage.

By the application of the methods above described, material was at hand consisting of 700 Items (leaves), representing 35 Samples (trees, each being a numbered botanical collection, now deposited in the herbarium of the New York Botanical Garden), further representing 4 assumed Populations (Upland White, Upland Red, Upland Blue, and Akalche Red), later to be compared as 4 Population-pairs (Upland White-Upland Red, Upland White-Upland Blue, Upland Blue-Upland Red, and Upland Red-Akalche Red).

OBTAINING THE BASIC DATA

All measurements on each Item were made to the nearest millimeter with a celluloid metric scale. Work sheets were prepared and data recorded which led either directly or indirectly to a characterization of the following 6 Features (fig. 1):

1. Blade-length. The full length of the leaf-blade was measured from the point of attachment of the petiole to the leaf-tip. Although the leaf-blade base in *Achras zapota* is generally acute, no difficulty was experienced in determining its terminus. In some leaves, one side extends proximally for a measurable distance more than the other side. In such cases, measurement was begun half-way along the extension. Frequently the midrib of the leaf was slightly curved, so that an exact measurement of its length was difficult. If the curve was definitely at one end or the other, a correction was per-

mitted by placing the metric scale along a hypothetically straightened line; if a slight curve occurred throughout, a correction was estimated.

2. Midlength-width. The width of the blade at a point midway along its length is always obtainable without difficulty, since the margins of the leaf are entire and never sinuate except when diseased.

3. Greatest-width. The greatest-width is described as occurring either at the midlength, or proximally or distally from it. Furthermore, it can occur at one particular point along the length, or it can extend along the leaf for various distances. In *Achras*, when the greatest-width was not at midlength, it was measurable at a point; when the greatest-width was at midlength, it sometimes extended proximally or distally, forming a leaf with partly parallel sides. When such parallel sides were largely distal from the midlength—giving the illusion of its being oblanceolate—the shape is here referred to as abelliptic; when such sides were proximal, the shape is adelliptic.

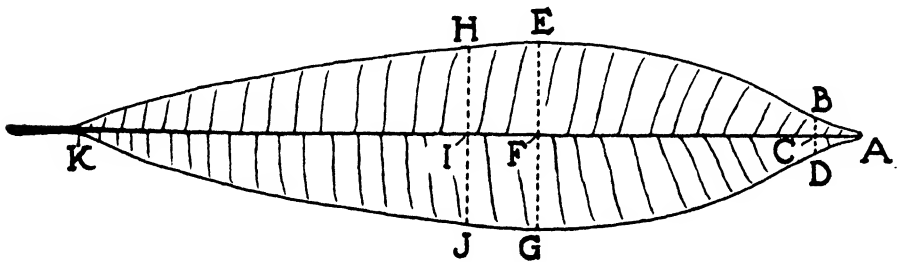


FIG. 1. Diagram of a leaf of *Achras zapota*, showing the 6 Features investigated in this study. Blade-length, AK. Midlength-width, HIJ (I is at midlength). Greatest-width, EG. Degree of lengthwise eccentricity, FI/AK. Degree of breadthwise eccentricity, (EG-HJ)/HIJ. Apex-width, BD (AC, 1 cm.). Drawing by L. Partelow, Draftsman, Syracuse, N. Y.

4. The Degree of Lengthwise Eccentricity (DLE). This Feature was developed in order to obtain a serviceable measure of the departure of the greatest-width from the midlength, i.e., the degree to which the greatest-width approached either end of the blade. The distance was measured along the midrib between the midlength and the greatest-width. This figure was converted to a percentage by dividing by the full blade-length.

5. The Degree of Breadthwise Eccentricity (DBE). Comparable to DLE, DBE is designed to express the increase in width of a leaf beyond the width it possesses at midlength. The difference between midlength-width and greatest-width is computed. This figure is divided by the midlength-width in order to give a percentage which can be considered in relation to that midlength. Expressed as a formula,

$$DBE = \frac{(\text{greatest-width}) - (\text{midlength-width})}{\text{midlength-width}}$$

6. Apex-width. The type of apex is frequently distinctive of different populations of plants. It is frequently referred to as being rounded, obtuse, acute, acuminate, or attenuate, and emarginate or apiculate. In the populations studied, all leaves were emarginate, although some were conspicuously more so than others. For purposes of quantitative measurement of the nature

TABLE 1. *Leaf-shape types in the 35 samples of Achras zapota.*

Bot. coll. no.	Number of leaves in each leaf-shape type				
	Oblanceolate	Abelliptic	Elliptic	Adelliptic	Lanceolate
42-137	9	3	3	4	1
42-138	11	5	4	0	0
42-139	8	6	5	1	0
42-140	15	1	4	0	0
42-141	15	2	3	0	0
42-142	19	1	0	0	0
42-143	13	3	4	0	0
42-144	6	8	5	1	0
42-145	15	2	3	0	0
42-146	12	7	1	0	0
42-148	16	3	1	0	0
42-149	4	6	10	0	0
42-150	2	3	11	4	0
42-151	8	5	7	0	0
42-152	11	5	4	0	0
42-153	3	8	5	4	0
42-154	11	7	2	0	0
42-155	1	6	11	2	0
42-156	17	2	1	0	0
42-157	8	6	6	0	0
42-158	13	5	2	0	0
42-158A	7	7	5	1	0
42-159	11	4	4	1	0
42-160	6	5	8	1	0
42-161	11	4	5	0	0
42-168	8	4	6	2	0
42-169	7	8	4	1	0
42-170	15	4	1	0	0
42-171	12	6	2	0	0
42-172	16	3	1	0	0
42-173	4	7	7	1	1
42-174	6	8	6	0	0
42-175	15	5	0	0	0
42-176	10	7	3	0	0
42-177	20	0	0	0	0

of the leaf tip, the concept of apex-width was developed, and now defined as the width of the leaf 1 cm. from the tip. This distance is correlated with such qualitative terms as rounded, acute, and attenuate. It is not to be overlooked, however, that it ignores the condition of the sides of the triangle of which the apex-width is the base. Such sides may be straight, concave, or convex, each resulting in a distinctively appearing tip.

THE DATA AND ANALYSES

All calculations in this study were carried out for the author by Hartley K. Phinney, New York State College of Forestry, with the exception that figures for DLE and DBE in table 1, Items 1 through 160, are by Mrs. Dorothy Thomson of Belize, British Honduras.

Characteristics of the Items. According to the methods outlined above, data have been obtained concerning the 6 Features for each of the 700 Items. These were utilized in the computations presented in tables 2-4.

Characteristics of the Samples. Each Sample (tree) contains 20 Items (20 leaves). The leaf-shape types within each Sample are summarized in table 1. Furthermore, for each of the 35 Samples, 3 characteristics have been computed for each of the 6 Features. These are: (1) the *mean* of the measurements; (2) the *range* of the measurements; and (3) the *standard deviation* of the measurements. These statistics are presented in table 2.

Characteristics of the Populations. For each of the 4 Populations, Upland White, Upland Blue, Upland Red, and Akalche Red, 3 characteristics have been computed for each of the 6 Features. These are: (1) the *mean of the sample means*; (2) the *observed range of the sample means*; and (3) the *standard error of the sample means*. These statistics are presented in table 3.

Characteristics of the Population-Pairs. For each of the 4 Population-pairs, 3 characteristics have been computed for each of the 6 Features. These are: (1) the *difference between means of sample means*; (2) the *standard error of the difference between means of sample means*; and (3) the ratio *t*. These statistics are presented in table 4.

SIGNIFICANCE OF THE VALUES OF *t*

The 24 values of *t* computed in the preceding section have been compared to their respective 5 per cent and 1 per cent levels and adjudged "non-significant" or "significant" at each level, according to D. D. Paterson, "Statistical Technique in Agricultural Research," New York, N. Y. Twenty-three of the values were found non-significant; only one was significant, as shown in table 4.

In each instance of non-significance of *t*, it may also be said that the respective difference between means of the 2 Populations is too small to be considered significant. Further evidence is necessary to determine if the mean actually indicates 2 distinct Populations of the respective Feature. Until that time it may be assumed that the difference is only an incident of sampling from a single normally variable Population.

The single instance of significance of *t* at the 5 per cent level indicates a significant difference between blade-length means of Upland Red and Upland White Populations. From another point of view, this value of *t* indicates that the relatively wide difference of means will occur—assuming

TABLE 3. *The characteristics of the 4 populations.*

Population	No. of sample means	Features											
		Blade-length, cm.			Midlength-width, cm.			Greatest-width, cm.			DLE, ^d per cent		
		Mean ^a	Range ^b	Stand. error ^c	Mean	Range	Stand. error	Mean	Range	Stand. error	Mean	Range	Stand. error
Upland White	10	10.50	5.60	0.50	3.92	1.46	0.15	3.97	1.37	0.15	3.83	9.84	1.06
Upland Blue	5	11.56	3.55	0.67	4.38	1.37	0.26	4.44	1.34	0.26	5.88	2.97	0.56
Upland Red	10	11.78	2.99	0.29	4.21	2.23	0.20	4.32	2.50	0.22	6.67	11.21	1.04
Akache Red	10	10.65	4.10	0.46	3.86	1.71	0.18	3.94	1.68	0.17	5.63	7.94	0.86
											1.29	3.12	0.31
											1.69	0.76	0.13
											2.34	4.85	0.49
											1.98	3.97	0.39
											1.92	1.40	0.13
											2.02	0.30	0.06
											1.84	1.98	0.19
											1.83	0.80	0.07

^a Mean of the sample means.^b Range of the sample means.^c Standard error of the sample means.^d DLE, degree of lengthwise eccentricity.^e DBE, degree of breadthwise eccentricity.

identity of Upland Red and Upland White Populations—in not more than 5 per cent of any sample Population-pairs examined. On the basis of closer correlation with the published *t* values, this difference will occur in about 4 of every 100 sample Population-pairs.

CONCLUSIONS

All differences in midlength-width, greatest-width, DLE, DBE, and apex-width within each of the 4 Population-pairs are too small to be considered significant. All differences in blade-length are non-significant also, except the difference between the Upland Red and the Upland White Populations, which is sufficiently large that it will occur in only 4 of every 100 pairs—assuming identity of the Upland Red and the Upland White Populations. This difference in blade-length means (actually only 1.28 cm., with a range of means among the Upland Red trees from 10.32 to 13.31 cm., and among the Upland White trees from 8.89 to 14.49 cm.) is by itself too small to be of importance to the plant taxonomist, and cannot be used for the practical segregation of taxonomic units.

In conclusion, therefore, further evidence is necessary to determine if the observed differences in leaf Features actually indicate that the Upland White, Upland Red, Upland Blue, and Akalche Red groups are distinct taxonomic Populations. Until that time it may be assumed that the differences are only incidents of sampling from a single normally variable Population, and that the *zapote blanco*, the *zapote colorado* of upland and of akalche, and the *zapote morado*, as occurring in northern British Honduras, are conspecific.

The characterization of the leaves of this entire Population of 35 trees, as expressed by the means, ranges, standard deviations, and standard errors of tables 2 and 3, are estimates of the normal variation of the species. Such statistics can serve as a basis of reference for the future study of variation in normal *Achras* leaves in other parts of tropical America, especially in regard to other Populations that may be thought significantly different.

NEW YORK, N. Y.

**SUPPLEMENTARY NOTES ON ARCTIC AND BOREAL
SPECIES IN BENSON'S "NORTH AMERICAN
RANUNCULI"**

NICHOLAS POLUNIN

In recent issues of the BULLETIN¹ Dr. Lyman Benson of the University of Arizona has published a noteworthy series of five papers on those members of the genus *Ranunculus* which he recognizes as occurring in North America north of Mexico and including Greenland. From data which I have accumulated during field and herbarium studies extending over a period of more than thirteen years I should like, however, to add the following remarks about the more northerly ranging of these and some related entities. Further details concerning most of them may be found in my "Botany of the Canadian Eastern Arctic, Part I, Pteridophyta and Spermatophyta,"² hereafter cited as "Bot. Can. E. Arctic I," or in "Part IV, Subarctic Regions," which now seems unlikely to be completed until after the war.

Had Dr. Benson made it clear in his papers that his "conservatism in assigning ranges . . . is in part a matter of policy" (Benson in lit.), some at least of these notes would have been superfluous; in the absence of any such statement made publicly they are all the more called for. Dr. Benson's "belief that the published range . . . should be based upon the specimens the author has been able to examine himself" (Benson in lit.) is to be commended so long as it does not cramp the subject or seriously derogate the work of others and is moreover the stated reason for ignoring previous authoritative reports. In the absence of such a clear statement of policy the reader will be apt, and rightly, to expect all pertinent material to have been consulted, the previous reports if ignored to have been proved wrong, and the given range in the absence of any admission of doubt to be that known at the time of publication. Any lesser statement may be as misleading as, unfortunately, indiscriminate citation of ranges "from the literature" is liable to be. And so it is with ecological habitats: one cannot rely on obtaining from occasional notes on herbarium labels a true conception of their ranges in the Arctic without knowing what any of those vast and variable regions are really like. Meanwhile it may be noted that I, too, when citing or repeating a report for which I have seen no supporting specimen assume it to be worthy of remark and investigation rather than necessarily correct—unless it is of a "non-critical" plant by a usually reliable, modern author.

¹ Bull. Torrey Club 68: 157-172; 477-490; 640-659. 1941. 69: 298-316; 373-386 1942.

² Nat. Mus. [Canada] Bull. 92, i-vi, 1-408. 1940.

Dr. Benson's interpretation of many of the taxonomic entities he accepts or disallows is unexpected; but with such matters of opinion, as with inconsistencies in capitalization, for example, I am not at present concerned.

In writing thus I do not intend, where critical, to be so in other than a constructive and purely impersonal manner. Nor do I wish to detract from the value of Dr. Benson's original observations and considered opinions but rather to make them the more usable. To such ends and in an attempt to guard against the repetition of certain errors and misconceptions I offer the following supplementary notes on those species (and a few others) with which my own studies have been concerned: to facilitate reference each species is introduced by a citation of the page on which it is treated by Dr. Benson within the two cited volumes of this journal.

Vol. 68, p. 159. *Ranunculus acris* L. (s.l.) is also widespread in Asia. Whatever its position on the American mainland may be, it appears to be indigenous in Greenland as well as in Iceland (cf. M. P. Porsild, Medd. Grönl. **92**(1): 30. 1932). In Iceland as in Lapland it is to be found high up in the mountains, however little visited these may be. There seems, fortunately, to be no need to change the original (and evidently intentional) Linnaean *acris* to "acer," since the former rendering, although somewhat inelegant, was used as a masculine by Quintus Ennius (239-170 B.C.) and also by Columella and many subsequent "writers of good Latin." Dr. Benson employed the Linnaean *acris* but this has been so frequently changed (particularly of late on the Continent of Europe) that I felt prompted to consult several of Oxford's most eminent classical scholars on the subject; all agreed that Linnaeus's rendering was legitimate and should be retained (see *International Rules of Botanical Nomenclature*, ed. 3, Art. 70, 1935, and cf. p. 142, where "*Ranunculus acris*" is given as the "Proposed Standard-Species" of the genus).

Vol. 68, p. 649. *R. pedatifidus* J. E. Smith apud Rees, Cyclop. **29**(2) *Ranunculus* No. 72. 1814 (not 1819; see Jour. Bot. **34**: 311. 1896). This is admittedly a bad complex, but, at least in the sense in which it is understood by Dr. Benson (who includes both *R. affinis* R. Br. and "its" var. *leiocarpus* Trautv. among other synonyms), it occurs in Spitsbergen as well as in northern Asia and America (including Greenland), and is thus virtually circumpolar in range (cf. Fernald, *Rhodora* **36**: 94. 1934; and Bot. Can. E. Arctic I, 221, where additional ecological habitats are described). It has also been found in the Canadian Arctic Archipelago northwards to Harbour Fjord on the south coast of Ellesmere Island (Simmons, Vasc. Pl. Fl. Ellesmereland, 107. 1906), whence specimens are to be seen in the British Museum, Kew, and Copenhagen Herbaria. (Specimens supporting very many of my other statements can readily be seen in the Gray Herbarium of Harvard University or in some other major American institution.) Dr. Benson states that the type material of *R. affinis* came from Melville Island, but this is hardly

allowed for by the range "Yukon to Baffin Island, Labrador . . ."; nor is it necessarily true, it has seemed to me from a recent perusal of Parry's *Journal* in the light of all available facts (cf. Jour. Bot. 80: 87. "1942"). Again, "chiefly in the vicinity of Winter Harbour" refers to the *totality* of "Plants observed in Melville Island . . . by the Officers of the Expedition" (R. Brown in Suppl. App. Parry's "Voyage for the Discovery of a North-West Passage, in the years 1819-20," cclxi. 1824); it does not necessarily mean that *R. affinis* was collected at this place, however probable that may seem; nor is it likely that this plant, which is generally uncommon in the Far North, was collected by all of the officers mentioned! The related *R. auricomus* L. and its "var. *glabrata* Lynge" have been reported from East Greenland (Sørensen, Medd. Grøn. 101(3): 53-4. pl. 2, 3. 1933). Concerning this question of whether or not *R. auricomus* occurs in North America, Dr. Benson (in lit.) agrees that although "the older reports were based upon confusion with other species" these of Sørensen may well prove to be correct. According to Britton & Brown (Ill. Fl. ed. 2, 2: 104. 1913), *Ranunculus auricomus* is the type species of the genus.

Vol. 68, p. 649. *R. Sabinii* R. Br., named after Captain Edward Sabine, and, like *R. affinis*, published in the *Supplement* to the Appendix to Parry's "1st. Voyage," with little doubt occurs also on the mainland coast of North America (Hooker, Fl. Bor.-Am., 1: 17. 1829; Macoun & Holm. Rep. Can. Arctic Exp. 1913-18, 5(A): 13. pl. 5, f. 4. 1921). It is also *said* to reach the Rocky Mountains (Britton & Brown, Ill. Fl. ed. 2, 2: 108) and southward to Montana (Davis, Minn. Bot. Studies, II. 4: 489. 1900, sub nom. *R. pygmaeus* var. *Sabinii*) or Nevada (Simmons, Vasc. Pl. Fl. Ellesmereland, 112. 1906), and has even been reported from the Taimyr Peninsula, Siberia, by Tolmatchew (Compt. Rend. Acad. Sci. U.R.S.S., A, No. 5, 108. 1930). Whether or not these claims can be substantiated it should be noted that according to Simmons (Vasc. Pl. Fl. Ellesmereland, 113. 1906), who has probably observed more *R. Sabinii* in the field than any other botanist, it "prefers the fields of stiff clay." With regard to the above rendering of the specific name, it now appears that the many authors (including myself in Bot. Can. E. Arctic I) who have changed it to "Sabinei" have done so unjustifiably, as Robert Brown's original "Sabinii" was not a "clearly unintentional orthographic error" (*International Rules*, Art. 70) but apparently a form of Latinization which he later repeated (e.g., in *Pleuropogon Sabinii*) and to which many of his contemporaries adhered.

Vol. 68, p. 652. *R. Allenii* Robinson I have recently found as far west as Port Harrison (lat. 58° 26' N) on the east coast of Hudson Bay. Towards its northern known limits it appears to be confined to grassy or mossy gullies and depressions, or sheltered banks which are likewise deeply invested with snow in winter and remain damp through much of the summer. The relationships of this to the last species and, through it, to the next three listed below

are still in need of elucidation (see Bot. Can. E. Arctic I, 219–20). Even if Robert Brown's actual statement concerning *R. Sabinii* (Suppl. App. Parry's "1st Voyage," cclxiv. 1824) was "*Planta inter R. nivalem et pygmaeam media in Herb. D. Sabine exstat*" (sic), it seems to me that *R. sulphureus* should be substituted for the former parent if *R. Sabinii* is indeed of hybrid origin.

Vol. 68, p. 656. *R. nivalis* L. In my experience this species is more characteristic of temporarily inundated areas below melting banks of snow and of mossy slopes where there is little competition from herbs of ranker growth than of "Arctic-alpine grassland" which, at least in any form that is familiar and thus termed farther south, is scarcely developed in the Far North. Not only is this term of problematical value, whether it be used for a habitat or for a general zone, but it can be rather misleading when applied to truly arctic regions. In English we should avoid unwarranted Germanisms and write Wolstenholme (not Wohlstenholme), Spitsbergen (not Spitzbergen), etc. In all of the thousands of living examples that I have seen, the fresh flowers of this species were bright yellow, becoming lighter in colour only when faded (contrast Britton & Brown, Ill. Fl. ed. 2, 2: 107, whose figure is also rather misleading).

Vol. 68, p. 656. *R. sulphureus* Solander apud Phipps, Voy. N. Pole, 202, 1774. Why "perhaps Iceland"—when so many reports of other species have been entirely ignored? I must take the liberty of refuting the contention that this species should be credited to Phipps alone, as the description was contributed by Solander. This is indicated by a MS belonging to the Department of Botany of the British Museum (Solander MSS, vol. 12, genus 2854). According to Mr. J. E. Dandy (in lit.), who was kind enough to make and send me from their war-time place of greater safety a copy of this MS and also of that of *Agrostis algida* (Solander MSS, vol. 3, genus 361), there can be "little doubt that the slips kept by Solander . . . were not part of the MS sent to Phipps but were Solander's own original notes which he kept for his personal use." Thus these notes "contain numerous erasures, alterations, and additions"; to them have later been added the page citations in "*Phipps it.*"; and in the published version there appear further notes on the systematic position of the plants instead of the place of collection, which was evidently considered unnecessary in a work on Spitsbergen. The only other major changes in the published version are in the sequences of words; but Mr. Dandy remarks (in lit.) that "Solander has placed small figures over the words of his MSS which apparently indicate the revised order which, after consideration, he preferred for publication." Thus were the plants of Phipps' "Voyage towards the North Pole," like many others of the day, identified and described not by a ship's captain but by "Linnaeus' favourite pupil" and Banks' assistant Solander, concerning whose MSS Mr. A. J. Wilmott, Deputy Keeper, Department of Botany, British Museum, affirms

(in lit.) that positive knowledge of the relationship between them and the publications to which they gave rise has existed continuously in some quarters. Mr. Wilmott also contends that the case of *R. sulphureus*, like that of *Agrostis algida*, is covered by Art. 48 of the *International Rules* which state that "Where a name and description by one author are published by another author, the word *apud* is used to connect the names of the two authors. . . ." As regards the type locality, this is not Low Island (off the coast of North East Land), but, according to Solander's MS notes, "prope Smierenberg" [in the north-west of the Spitsbergen archipelago, probably on Amsterdam Island; see Lynge, Skr. Norske Vidensk.-Akad. I. Mat.-Nat. Kl. **1938** (6): 7] where, on Phipps's return voyage, a fairly protracted stay was made for scientific work, and where "Dr. Irving climbed up a mountain" (Phipps, Voy. N. Pole, 69). In this exposed region *R. sulphureus* is not infrequent and may be expected to be particularly plentiful in some situations; for, as I have noted in the course of my own travels there, an unusually large proportion of the lowland is occupied by the "boggy tundra" of which, at least in Spitsbergen and the Canadian Eastern Arctic, the present species is far more characteristic than is *R. nivalis* (contrast Benson l.c.).

Vol. 68, p. 657. *R. pygmaeus* Wahlenb. In my material the petioles of the radical leaves, although usually "1-3.5 cm. long," are sometimes 4 or even 5 cm. in length. Again I would emend the "Arctic-alpine grass-land," as this tiny plant in the American Arctic is largely restricted to the little-vegetated inner zones of late-lying snow patches where few other phanerogams persist and where the growing-season is so short that grasses, if any occur, are usually of insignificant development and fail to flower (apart from the diminutive "*Agrostis algida*" Solander *apud* Phipps). Farther south such habitats, and in them frequently *R. pygmaeus*, are found chiefly at rather high altitudes, e.g., in southwestern Greenland and in Iceland and northern Lapland. Neither in any of these places nor in far northern Canada or Spitsbergen have I ever seen the "pigmy buttercup" inhabiting "meadows"; it is remarkably intolerant of competition from larger plants, and, even in the Arctic, almost all vascular plants and many cryptogams are larger than it! In a recent paper (Am. Jour. Bot. **29**: 498. 1942) Dr. Benson has recorded *R. pygmaeus* var. *petiolulatus* Fernald and *R. verticellatus* Eastwood as confined, or nearly confined, to "Arctic Tundra" (as opposed to "Alpine Tundra" [sic] or other of his "subdivisions"). However, in proposing the variety Professor Fernald (Rhodora **19**: 138. 1917) expressly contrasted it with "typical *R. pygmaeus* of the Arctic regions, Labrador and the Canadian Rocky Mountains," while recently (Bull. Torrey Club **68**: 658) Dr. Benson indicated that this "var. *petiolulatus* Fern." (sic) was still known only from Mt. Albert, Gaspé County, Quebec: so evidently it ought to be excluded from the known flora of the Arctic. Somewhat similar remarks probably apply, though with less force, to *R. verticellatus* Eastwood; for Nome City (which is

not "at Cape Nome"), whence came the only known material of it (see Benson, Bull. Torrey Club **68**: 659), can scarcely be accepted as truly arctic. On the other hand, it would seem desirable to include in the flora of the truly arctic regions *R. kamchaticus* DC. and *R. Camissonis*³ Schlecht. (or, perhaps more elegantly, Schlechtend., not the misleading "Schlect"; Benson, Bull. Torrey Club **69**: 378-9, and cf. Am. Jour. Bot. **29**: 499); the former species reaches Port Clarence and the Teller Reindeer (not "Ranger") Station (cf. A. E. Porsild, *Rhodora* **41**: 165, 228. 1939) and the latter species is known from St. Lawrence Bay on the Siberian side and Cape Prince of Wales on the Alaskan side of Bering Strait, as well as from Little Diomedé Island between these two stations (A. E. Porsild, Trans. Roy. Soc. Canada III. Sect. 5, **32**: 30. 1938).

Vol. 69, p. 306. *R. Flammula* L. var. *filiformis* (Michx.) Hook. (*R. reptans* L.). I should have preferred to have followed Linnaeus (Sp. Pl. ed. 1, 549) and most subsequent authors in according this plant specific rank, even if it appears to "run into" *R. Flammula* in some places; otherwise we shall find ourselves, in the interests of consistency as botanical exploration goes on, prompted to unite more and more species which on most counts appear abundantly distinct. Whatever it be called, the present plant is circumboreal and wide-ranging latitudinally but except in Novaya Zemlya (Lyngé, Rep. Norwegian Exp. Nov. Zem. 1921, No. 13, 39. 1923) appears to reach only the southern fringe of the Arctic and there to be characteristic not so much of the "marshy ground of" lakes, streams, and ditches as of their actual beds, whether or not these dry out in summer (cf. Lyngé l.c.).

Vol. 69, p. 311. *R. hyperboreus* Rottb. The "Island of Grönland" is not only misquoted but seriously misleading. This species reaches all the major (and probably most minor) land-masses of the high-arctic regions and "varies greatly with the habitat, having long, trailing internodes and petioles when growing in water—in which case the leaves generally expand and float on the surface, so constituting in the Far North the only 'floating leaf' type. On dry land the whole plant is much condensed, rarely rising more than a few centimetres above the surface of the ground, and having short internodes and much smaller leaves" (Bot. Can. E. Arctic I, 211-213). The species is almost as common in pools or creeping on wet mud in the mountains as on "marshy ground . . . near the sea"; it is hardly a plant of "grassland," even where this is to be found in the Arctic. The var. *Turquetilianus* of my Bot. Can. E. Arctic I, 211. pl. 6, from the west coast of Hudson Bay, appears worthy of some mention.

Vol. 69, p. 312. *R. sceleratus* L. Also in Asia. Scarcely arctic or normally even subarctic, but not uncommon in freshwater pools at and around Churchill, lat. 58° 46' N on the west coast of Hudson Bay. Most individuals

³ The original spelling and apparently an intentional form of Latinization; cf. *R. Sabini* (above) and see Schlechtendal, *Animadv. Bot. Ranunc. Cand.* 1: 12, 30. 1819.

there grow from 20 to 30 cm. high and appear to belong to the typical form, but one collection which I made during my first visit to Churchill in 1934 has the leaf-characters of var. *multifidus* Nutt.

Vol. 69, p. 313. *R. Gmelini*⁴ DC. var. *terrestris* (Ledeb.) L. Benson (*R. Purshii* Richardson *op. cit.*, p. 741; not "Richards," "751"). Members of this complex of course occur outside of North America. The present one indeed persists, as Dr. Benson implies, well north in the West (cf. also Raup, Jour. Arnold Arb. 17: 254. 1936); at Churchill it is plentiful, growing luxuriantly and flowering and fruiting abundantly, while it also occurs somewhat farther north on the west coast of Hudson Bay, near the mouth of Seal River; see specimens in the New York State College of Agriculture at Cornell University and in the Herbarium of the Academy of Natural Sciences of Philadelphia.

Vol. 69, p. 314. *R. Gmelini* var. *yukonensis* (Britt.) L. Benson is given as "northern coniferous forest" and later affirmed (Am. Jour. Bot. 29: 499. 1942) as there "endemic or nearly so." According to Mr. A. E. Porsild (Rhodora 41: 229. 1939, sub nom. *R. Purshii* subsp. *yukonensis*), however, it would appear to extend far beyond the ill-defined limits of this "sub-division" of Dr. Benson's "circumboreal flora."

Vol. 69, p. 375. *R. Cymbalaria* Pursh. Plentiful on the west coast of Hudson Bay around Churchill, and long known from West Greenland; forms belonging to its complex occur also in Scandinavia and, according to Hultén (Hist. Arctic & Boreal Biota, 103. 1937), in South America.

Vol. 69, p. 379. *R. glacialis* L. The rather numerous claims of this species from arctic Canada are apparently all without foundation (cf. Bot. Can. E. Arctic I, 215-8). It is unknown from West Greenland, although widespread on the east coast (cf. *R. auricomus* above).

Vol. 69, p. 381. *R. aquatilis* L. var. *capillaceus* (Thuill.) DC. (*R. trichophyllus* Chaix apud Vill.). At least in the sense in which it is upheld by Dr. Benson (i.e., as including *R. subrigidus* W. B. Drew), this is plentiful and grows luxuriantly at Churchill on the west coast of Hudson Bay; some of my material from there was verified by Dr. Drew himself as belonging to *R. subrigidus*. Quite possibly referable here, too, are some of the representatives of the complex that occur in West Greenland (see below); others inhabit the southern hemisphere.

Vol. 69, p. 383. *R. aquatilis* var. *eradicatus* Laestad. (*R. trichophyllus* var. *eradicatus* [Laestad.] W. B. Drew). Also found in shallow eddies in streams. Persists far north of the line indicated by "Quebec to Labrador and Newfoundland" and also well north of any zone of extensive consolidated "grassland." So variable in S. W. Greenland that I am still uneasy about my disposition of some of the forms that I collected in the Julianehaab dis-

⁴ The original spelling, which in this instance must be retained; see *International Rules* (as opposed to *recommendations*).

triet in 1937; meanwhile it should be noted that, from farther north in West Greenland, Dr. M. P. Porsild (Medd. Grøn. **58**: 77. 1920) has "with some hesitation" claimed *R. divaricatus* Schrank, whose synonymy suggests that the plant in question may well have been *R. aquatilis* var. *capillaceus* (*R. trichophyllus* var. *typicus* W. B. Drew, *Rhodora* **38**: 18. 1936), which is at least approached in the Julianehaab district (see above and in Jour. Linn. Soc. **52**: 385. 1943).

Vol. 69, p. 385. *R. Pallasii* Schlecht. This peculiar plant occurs also in the Canadian Arctic Archipelago (about 8 miles inland of Lake Harbour, Baffin Island; see Bot. Can. E. Arctic I, 210-211). Long known from Spitsbergen, Novaya Zemlya, and continental Eurasia; possibly circumpolar.

Vol. 69, p. 385. *R. lapponicus* L. Also known from several parts of Baffin Island in the Canadian Arctic Archipelago (see Bot. Can. E. Arctic I, 214).

While I feel with Dr. Benson (cf. also Am. Jour. Bot. **27**: 807. 1940) that these last two species are so distinctive as almost to demand erection as monotypic subgenera, I cannot help recalling that, at least in Spitsbergen, they appear to hybridize rather freely; cf. also Resvoll-Holmsen, *Svalbards Flora*, 40 (1927). However, we do not necessarily "lump" those genera of grasses, for instance, which are inter-fertile! With regard to the charming and appropriate name *Coptidium*, it seems clear that this should in the first instance be credited to Beurling (or, in view of the Amsterdam Congress changes in the *International Rules*, perhaps to Beurling ex Nyman) instead of to Nyman, though Dr. Benson (l.c.) may well be right in claiming it as his own (positive) *subgenus*. Thus Nyman already cited Beurling ("V. *Coptidium* (Beurl.) . . . C. *ranunculoides* Beurl.") in his Consp. Fl. Eur. **1**: 13 (1878), and this inadequate citation presumably had reference to Beurling's much earlier but frequently overlooked "Plantae vasculares seu cotyledoneae scandinaviae. . . ." 1-69 (1859), on page 1 of which the name occurs twice. The first time it is used as a sectional (or subgeneric?) name immediately following the generic heading, as follows: "Ranunculus Linn. a. ? *Coptidium*. 1. *R. lapponicus* Linn." This is followed by "b. *Euranunculus*," there being only the one species under *Coptidium*. The query apparently expressed the author's uncertainty as to whether *Coptidium* should not be upheld as a separate genus, or as a subdivision under *Coptis*, for the second occurrence of the name in this publication is as a generic one in a footnote (no. 10) following the "*R. lapponicus* Linn." quoted above. This footnote reads as follows: "*Ranunculis* socius invitus, familiarior *Coptidi*. *Coptidium ranunculoides* Beurl. in herbar. propr." (cf. Nyman, Consp. Fl. Eur. **1**: 13, but contrast Ind. Kew. **1**: 611).

A REPLY TO DR. POLUNIN

LYMAN BENSON

Dr. Nicholas Polunin's article entitled "Supplementary notes on Arctic and boreal species in Benson's 'North American Ranunculi'" is concerned primarily with habitat notes and range extensions based in part upon field studies in the eastern Canadian Arctic but largely upon published notes concerning the occurrence of species and varieties. He criticizes my work chiefly because I have not relied upon such notes and particularly upon those in his "Botany of the Canadian Eastern Arctic" in determining the ranges of species. However, he admits at the close of the introduction, ". . . I, too, when citing or repeating a report for which I have seen no supporting specimens assume it to be worthy of remark and investigation rather than necessarily correct. . . ."

My conservatism in assigning ranges not only to Arctic species but to all others is a matter of basic policy. It is my belief that in such papers as these the published range of a species or a variety, unless occasionally noted otherwise, should be based upon the specimens or living plants the author has been able to examine himself. Examples are as follows:

1. *R. PEDATIFIDUS* J. E. Smith. Exact definition of this species is still a puzzle, and I should not attempt it without seeing more Old World material (practically impossible at present). Some of the Asiatic material I have seen indicates great variability, and I have seen only enough to convince myself that the group needs study. My conservatism in assigning it a range reflects caution in dealing with an entity or group of entities in need of better definition, and it accounts for omitting Spitzbergen, since I have seen no material from there. In short, I have given only the range I know to apply to what I have believed to be *R. pedatifidus*, and I have taken no chance on confusion with other types.

2. *R. SABINII* R. Br. Despite the note in Britton & Brown's *Illustrated Flora* (cited by Polunin) to the effect that *R. Sabinii* occurs in the Rocky Mountains, I know of no reason to believe that it does. Of course, it is possible that, in reorganizing the *Ranunculi* at the New York Botanical Garden while I was there on a fellowship in the summer of 1935, I overlooked the specimens Britton had in mind or overlooked recording them. Many *Ranunculi* which do not occur there have been reported from the Rocky Mountains, and, as a matter of fact, allowing northern species an extension into the Rockies is much more common than the facts would warrant, despite the relationship of the boreal flora to that of the Rocky Mountain System (cf. L. Benson, *Am. Jour. Bot.* **29**: 494. 1942). Davis' monograph of the North

American *Ranunculi*, published in 1900 and cited by Polunin to the effect that *R. Sabinii* occurs in Montana, seems to be largely a compilation. The chances of the plant's occurring in Nevada may be one in a hundred, at most.

3. *R. AURICOMUS* has been reported a number of times to occur in North America, but the older reports were based upon confusion with other species. I see no reason why the plant should not be found to occur in Iceland or Greenland, and I have no reason to question Sørensen's identification of his specimens, but still I do not believe I should accept such reports without seeing the specimens myself. This does not reflect in any way upon the authors of the many notes I have come across in the literature, for in numerous cases, which I have been able to investigate, the notes are correct. However, the genus *Ranunculus* is a difficult one, and my interpretation of many entities is new. Consequently, I have not felt it advisable to accept anyone else's interpretation of a plant as being necessarily identical with my own. The result in many cases is understatement of the actual range of a species despite published notes to the contrary. A study of the confusion of names on specimens of *Ranunculus* in practically any large herbarium should be adequate to show the necessity for this policy. Except in a few especially well kept local or regional herbaria, the number of names in agreement with those I have selected is probably less than 35 per cent, although many of the names actually used are synonyms. The confusion of plants reported in the literature is not so great, but experience has shown it to be considerable.

4. *R. CYMBALARIA* Pursh. According to Polunin “. . . long known from West Greenland; forms belonging to its complex occur also in Scandinavia and, according to Hultén . . . , in South America.” The folly of adding this sort of a synthetic range to *R. Cymbalaria* should be obvious from the following: (1) The type occurring in West Greenland is most likely to be not typical *R. Cymbalaria* at all but the var. *alpina*. (2) I have seen no specimens from Scandinavia, but the fact that they belong to the same complex as *R. Cymbalaria* is neither here nor there. In my personal herbarium and elsewhere there are numerous collections of members of the complex from Tibet, the Himalaya Mountains, and western China, but none of these is typical *R. Cymbalaria*, and some seem to represent a separate species while others seem to be between the typical variety and var. *alpina* in many ways but with characters of their own. The Scandinavian plants may be more closely related to these Asiatic ones than to *R. Cymbalaria* or different from either. (3) The South American plant is *R. tridentatus* H. B. K., distinctly different in the specimens I have seen from *R. Cymbalaria*, but related to it.

In the discussions of *R. nivalis* and *R. pygmaeus* and elsewhere, Dr. Polunin takes exception to the term “Arctic-alpine grassland.” It is to be noted that I have abandoned it already (*Am. Jour. Bot.* **29**: 494, 1942), and in view of this I did not suppose he would wish to bother with further dis-

cussion. The references to vegetation types appearing in the articles in this BULLETIN are either the divisions recognized by Shantz and Zon (Natural Vegetation, Atlas of American Agriculture, U. S. Dept. Agr. 1924), or slight modifications of them. Shantz and Zon dealt only with the United States, and "Arctic-alpine grassland" is merely an extension of their term "Alpine grassland." I agree with Doctor Polunin that the term is inapplicable. On the other hand, I am not wholly certain that "Arctic tundra and grassland" would not be a better term than "Arctic tundra," the term I have adopted more recently. Use of the term "tundra" in the more recent publication is an adaptation from Weaver and Clements (Plant Ecology, ed. 2, 1938). As it is used here "Arctic" does not mean about the Arctic Sea or within the Arctic Circle. It refers to a broad vegetational area. Dr. Polunin has overlooked the fact that whatever term may be employed is adopted to refer to the general region above or beyond timber line and the meadows about timber line and not to the habitat of the specific plant. As an example from another vegetation type, a particular species occurring in the western United States may grow in some places among quaking aspens, yet we might designate it as a plant characteristic of yellow pine forests as opposed to sagebrush desert, juniper-pinyon woodland, or oak woodland. This is because in many parts of the West the quaking aspen occurs largely in wet places surrounded by drier forests of *Pinus ponderosa*; in other words, although it may occur in pure stands, quaking aspen does not form a major vegetation type but merely indicates a local condition within a general type. My use of the term alpine tundra refers to the areas above timber line in the mountains of the Far West. *So far as Ranunculus is concerned*, the species occurring in the alpine areas of the northeastern United States and adjacent Canada are with those occurring beyond timber line to the northward. For this reason the areas in the Northeast are lumped with those of the far north, despite the fact that other elements of their included vegetation are not all in agreement with *Ranunculus*.

At various points (e.g. under *R. Allenii* and *R. hyperboreus*) Dr. Polunin bases criticisms upon matters quoted from the original statements of distribution of species and offered by the writer merely as material of possible help in determining the type collections. That under *R. hyperboreus* the data following the heading "type collection" should be taken as a statement of the known distribution of the species at present and criticized as misleading and inadequate and that in the discussion of *R. Sabinii* (under *R. Allenii*) similar data should be taken apparently as an argument concerning the hybrid origin of the species makes refutation of such points unnecessary.

It is with a feeling of disappointment that I find Dr. Polunin's valuable and long-continued observations on *Ranunculus* in the Arctic appearing

merely as a list of supplementary notes correlated with a review of my personal errors, such as accidental misstatement of a title, overlooking of two commas replacing periods after abbreviations, insertion of an unnecessary h in Wolstenholme, and omission of the newly published *R. hyperboreus* var. *Turquetilianus* Polunin because my note to the editor arrived too late to be inserted. Naturally I regret these errors, but I regret still more finding them used in an article in such a way as to overshadow the original observations of an eminent explorer and author.

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RESPONSE OF PYTHIOMORPHA GONAPODYIDES TO MANGANESE

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In experiments in this laboratory on the nutrition of fungi extensive use has been made of a medium containing magnesium sulfate, potassium dihydrogen phosphate, dextrose, and asparagine. This medium was used by Schopfer in his studies on *Phycomyces* (3), and in it *Phycomyces* grows quite satisfactorily if the chemicals used are of the customary C.P. grade. We have assumed that iron, zinc, manganese, and other supplementary mineral elements were furnished by the traces present as contaminants in the constituents of the nutrient solution. However, in most of our experiments we have added to the original medium a mixture of mineral supplements in order to insure their presence.

Although *Phycomyces* grows well in the unsupplemented medium we experienced difficulty in cultivating *Pythiomorpha gonapodyides* unless the mineral supplements were added. This difference in the response of two species of fungi indicated by our preliminary observations seemed worthy of further investigation. The results presented in this paper show that *Pythiomorpha gonapodyides* is especially sensitive to a lack of manganese.

MATERIALS AND METHODS

The fungi used were *Pythiomorpha gonapodyides*, *Phycomyces blakesleeanus* (+), and *Aspergillus niger*. The first two organisms have complete deficiencies for thiamine. *Phycomyces* grows if furnished the pyrimidine and thiazole intermediates of thiamine; *Pythiomorpha* is able to synthesize the thiazole portion of the thiamine molecule, but must be supplied with the pyrimidine half (1, 2). *Aspergillus* is autotrophic as far as thiamine is concerned.

All three fungi were grown at 25° C in 125-ml. Erlenmeyer flasks each containing 25 ml. of a basal liquid medium. The basal solution contained per liter, 1.5 g. KH_2PO_4 Sorensen (Mallinckrodt A.R.), 0.5 g. $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ (Mallinckrodt A.R.), 50.0 g. dextrose (Corn Products Co. C.P.), 2.0 g. asparagine and 400 μ moles of thiamine (Merek synthetic). The asparagine was purified by treatment with norit A and recrystallization from alcohol. The mixture of mineral supplements used was prepared by adding to 100 ml. of distilled water 5.7 mg H_3BO_3 , 15.7 mg. $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$, 140.4 mg. $\text{Fe}(\text{NH}_4)_2\text{SO}_4 \cdot 6\text{H}_2\text{O}$, 10.8 mg. $\text{Ga}_2(\text{SO}_4)_3 \cdot 18\text{H}_2\text{O}$, 8.1 mg. $\text{MnSO}_4 \cdot 4\text{H}_2\text{O}$, 3.6 mg. acid molybdic 85%, and 79.0 mg. $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$. The addition of 0.5 ml.

of this mixture¹ per liter of solution gave the following trace elements in p.p.m.: 0.005 B, 0.02 Cu, 0.10 Fe, 0.01 Ga, 0.01 Mn, 0.01 Mo, and 0.09 Zn. These quantities are later referred to as 1x supplements; twice these quantities, as 2x supplements, and one-fifth, as 0.2x supplements.

Bits of mycelium were used in inoculating cultures of *Pythiomorpha*. In the early experiments irregularities were observed which were traced to differences in the viability of the inoculum. For example, mycelium removed from the center of a colony frequently failed to grow. After some trials it was found that uniform results were obtained when the inoculum was taken from the edge of a colony 2 or 3 days old, grown in a liquid medium. Some further refinements in inoculation are given in connection with the individual experiments.

Dry weights were obtained by drying at 100° C after filtering the mycelium into Gooch crucibles and washing with distilled water, or by washing the mycelium with two changes of distilled water, pressing dry with the fingers and drying in aluminum pans.

All glassware was Pyrex. It was cleaned with chromic-sulfuric acid cleaning mixture, thoroughly rinsed with tap water and distilled water, and drained dry. The solutions were sterilized by autoclaving at 13 lbs. pressure for 25 minutes.

EXPERIMENTAL RESULTS

The Effect of Mineral Supplements on *P. gonapodyides*. In a preliminary experiment various amounts of the mineral supplements were added to the basal medium. The cultures were inoculated from a four-day-old culture grown in the basal medium plus 2x supplements. The pieces of

TABLE 1. Average dry weight (5 cultures) of *P. gonapodyides* grown 8 days in the solutions indicated.

Growth in the basal solution was the result of transfer of mineral supplements with inoculum. Compare with table 2.

Addition to basal solution	Av. dry wt. in mg.
No addition	30.0
0.2x supplements	41.0
1x supplements	79.3
2x supplements	44.3

inoculum were relatively large and no effort was made to remove the culture fluid retained by the mycelium used as inoculum. Dry weights of quintuplicate cultures were determined after 8 days growth (table 1). It appeared that the 1x amount of supplements was superior to the larger or smaller amounts.

¹ The mixture of mineral supplements is based on the work of Steinberg (4) with *Aspergillus niger*. Although boron has not been demonstrated to be required by the fungi it was added because of its essential character for higher plants.

However, greater growth occurred in the basal solution than was anticipated from earlier observations. This was because of the mineral supplements carried over in the inoculum, as was demonstrated by the lack of growth in the basal solution when special precautions were used to minimize the carry over. For example, *Pythiomorpha* was grown in the basal solution, and in the same solution plus 1x supplements. The basal solution was inoculated from cultures 3 days old grown in the basal solution. The solutions containing supplements were inoculated from cultures 3 days old grown in the basal solution plus 2x supplements. Pieces of inoculum were used about 2 mm. in diameter. These were taken from the edge of the colony and each piece was pressed against the side of the flask before it was transferred, in order to remove as much of the culture fluid as possible. Dry weights of quintuplicate cultures were determined after 48 hours incubation.

Under these conditions very little growth occurred in the basal solution while in the same solution to which the mineral supplements were added

TABLE 2. *Average dry weight (5 cultures) of P. gonapodyides in four successive passages in the solutions given.*

Period of growth in each passage, 48 hours.

Culture medium	Av. dry wt. in mg. in passage			
	1	2	3	4
Basal solution	0.4	0.0	0.8	0.0
Basal solution plus 1x supplements	3.9	7.7	9.9	12.7

the growth was quite satisfactory (table 2, Passage 1). Just before determining the dry weights at the end of the first passage subcultures were made from each of the cultures in the basal solutions to fresh flasks of the same medium. This procedure was followed also for the basal medium plus supplements. The fungus failed to grow in the second passage in the basal medium but produced a greater dry weight in the supplemented medium in the second passage than it did in the first passage. For the third passage in the basal medium inoculum was taken from the cultures of the second passage in the supplemented medium. Again growth in the basal medium was slight, but it was excellent in the basal medium plus supplements. An attempt was made to subculture the growth of the third passage in the basal medium without success, while a further increase in dry weight was obtained in the fourth passage in the supplemented medium (table 2).

This experiment, and others of the same character, demonstrated that *P. gonapodyides* would not grow in the basal medium prepared with chemicals of the purity customarily used in our laboratory provided suitable precautions were used to minimize the amount of the supplementary mineral elements carried over from the old to the new solutions in making inoculations.

The addition of a mixture of mineral supplements to the basal solution allowed growth to occur. Which of the elements in the mixture of elements was responsible for this effect?

Influence of Iron, Zinc and Manganese on *P. gonapodyides*. A deficiency of iron or of zinc was suspected to be responsible for the failure of *P. gonapodyides* to grow in the basal solution. Preliminary experiments showed, however, that the addition of iron or of zinc, or of both elements, failed to correct the deficiency. Manganese, however, proved to be decidedly beneficial. The following experiment in which the three elements were used alone, and in various combinations, illustrates these statements.

P. gonapodyides was grown in quintuplicate cultures in the basal medium, in the basal medium plus 1x supplements, plus iron, plus zinc, iron

TABLE 3. *Average dry weights (5 cultures) of P. gonapodyides grown in the solutions indicated for four successive passages.*

Period of growth in each passage, 48 hours.

Additions to basal solution	Av. dry wt. in mg. in passage			
	1	2	3	4
None	0.2	0.0
1x supplements	6.9	9.0	16.4	6.8
Iron only	0.2	0.0
Zinc only	0.1	0.0
Iron and zinc	0.3	0.0
Manganese only	3.8	6.1	12.3	3.8
Manganese and iron	3.4	5.0	9.6	2.8
Manganese and zinc	6.4	10.0	15.3	10.0
Manganese, zinc and iron	5.4	4.5	6.3	4.7

and zinc, manganese, manganese and iron, manganese and zinc, and iron, zinc, and manganese. The iron, zinc, and manganese were added as they existed in the 1x amount of supplements, that is, at 0.10 p.p.m., 0.09 p.p.m., and 0.01 p.p.m., respectively. The solutions were inoculated from cultures 3 days old grown in the basal solution plus 1x supplements using the precautions previously described to minimize the carry over. Dry weights were determined after 48 hours.

Growth was slight in the basal solution and in the basal solution supplemented with iron, with zinc or with iron and zinc together, and when transfers were made into the same solutions for the second passage no growth occurred in these media (table 3, Passage 1). Good growth developed in the solutions supplemented with manganese. Growth in the solutions supplemented with manganese and zinc was still better and nearly as good as that obtained when the complete mixture of supplements was used. The addition of iron to the solutions fortified with manganese or with manganese

and zinc reduced the growth somewhat, suggesting that the amount of iron used may have been above the optimum for this fungus. The results obtained in the first passage were in the main confirmed in passages 2, 3, and 4 (table 3).

In general our basal solution appeared to lack sufficient manganese for the growth of *P. gonapodyides*. When adequate manganese was supplied the further addition of zinc improved growth materially, but zinc without manganese was ineffective. Manganese and zinc together were about as satisfactory as the complete mixture of supplements. Again, as in the experiment summarized in table 2, growth improved in later passages as compared to that obtained in passage 1.

Optimum Amount of Manganese for *P. gonapodyides*. The optimum amount of manganese is probably affected by a number of factors; the

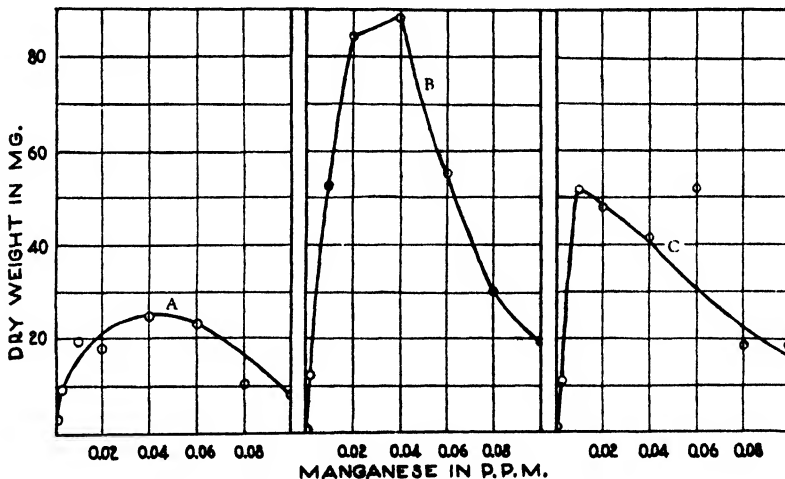


FIG. 1. Average dry weights (5 cultures) of *P. gonapodyides* plotted against the manganese added in p.p.m. to a basal medium. A, passage 2 (3 days growth); B, passage 3 (4 days growth); C, passage 4 (4 days growth).

presence of adequate amounts of zinc in the culture fluid may be important as well as temperature, the character of the inoculum, the time factor, the volume of the nutrient solution and other factors which need not be enumerated here. Although no attempt was made to study the influence of these various factors our results indicate that the optimum addition of manganese to our basal medium probably lies between 0.01 and 0.04 p.p.m. This is illustrated by the following experiment.

P. gonapodyides was grown in quintuplicate cultures in the basal medium and in the same medium plus 0.001, 0.01, 0.02, 0.04, 0.06, 0.08, and 0.1 p.p.m. of manganese added in the form of manganese sulfate. The cultures were inoculated from a culture two days old grown in the basal me-

dium plus 1x supplements. After 3 days of growth subcultures were made from passage 1 into similar media for passage 2. No dry weights were determined for passage 1. After 3 days subcultures were made for passage 3 and dry weights were determined for passage 2. For passage 3 the period of growth was 4 days, and for passage 4 it was 4 days. The results (fig. 1) show some unexplained irregularities, but indicate that with successive passages the optimum range for manganese tends to narrow and to be reduced. It seems probable that for the continued culture of this fungus the addition of 0.01 or 0.02 p.p.m. of manganese to our basal medium would be most favorable.

The quantity of manganese added to a single culture flask amounted to 2.5 μ g. for the media containing 0.01 p.p.m. Some growth through 4 successive passages was observed with the addition of 0.001 p.p.m. It is evident that 0.25 μ g. of manganese made the difference between failure to grow and continued survival.

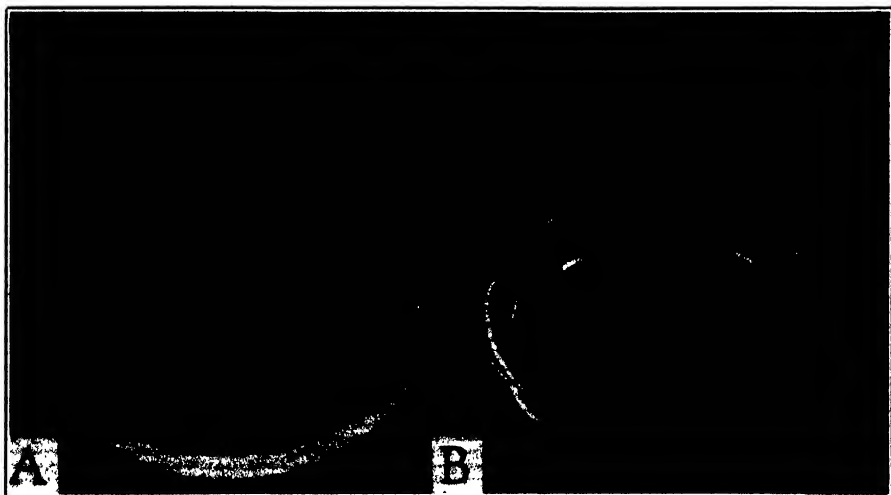


FIG. 2. *Pythiomorpha gonapodyides* growing in a basal solution with no added mineral supplements. A, medium prepared with Baker's analyzed magnesium sulfate; B, medium prepared with Mallinckrodt's magnesium sulfate analytical reagent. Age 5 days.

Presence of Manganese in C.P. Chemicals. In the course of our investigations excellent growth was obtained in one lot of the unsupplemented basal medium. It was found that in the preparation of this particular batch a sample of Baker's magnesium sulfate C.P. had been substituted for the Mallinckrodt magnesium sulfate A.R. which had been previously used. A further investigation demonstrated (fig. 2) that the Baker salt contained sufficient manganese to permit satisfactory growth of *P. gonapodyides*, but the amount in the Mallinckrodt preparation was inadequate. The manufac-

turers' printed labels gave the manganese content of the sample of Baker's magnesium sulfate as 0.002 per cent, of Mallinckrodt's magnesium sulfate as 0.0005 per cent.

Relative Effect of Mineral Supplements on *Pythiomorpha*, *Phycomyces*, and *Aspergillus*. The sensitiveness of *P. gonapodyides* to a deficiency of mineral supplements, especially manganese, suggested that the response of *Phycomyces blakesleeanus* and *Aspergillus niger* also should be determined under our conditions. It was found that both *Phycomyces* and *Aspergillus* grew quite satisfactorily in our basal solution through successive passages. For example, the average dry weights of quintuplicate cultures of *Phycomyces* in 4 successive passages in the basal medium (in which *Pythiomorpha* failed to grow) were as follows: 99.6 mg. (4 days growth), 118.8 mg. (5 days), 140.4 mg. (6 days), and 105.9 mg. (5 days).

TABLE 4. Average dry weights (4 cultures) of *Aspergillus niger*, *Phycomyces blakesleeanus* and *Pythiomorpha gonapodyides* in the third and fourth passages in a basal medium, and in the same medium plus manganese or a mixture of mineral supplements.

Period of growth in each passage 5 days.

Addition to basal solution	Av. dry wt. in mg. for					
	<i>Aspergillus</i> in passage		<i>Phycomyces</i> in passage		<i>Pythiomorpha</i> in passage	
	3	4	3	4	3	4
None	80.4	126.5	104.9	117.5	0.0	0.0
0.02 p.p.m. Mn	105.9	169.7	123.1	122.8	44.9	91.3
1x supplements	180.8	216.4	108.1	147.1	48.0	45.8

In another experiment the dry weights of the three fungi were determined in quadruplicate cultures in two passages (3 and 4) in the basal solution, in the basal solution supplemented with 0.02 p.p.m. of manganese, and in the basal solution plus 1x supplements. The period of growth in each passage was 5 days.

The procedure followed in preparing the cultures for which the dry weights are given in table 4 was as follows: A flask of each type of solution was inoculated by a bit of mycelium from a culture 2 days old grown in the basal medium plus 1x supplements. After 4 days subcultures were made from each type of culture medium into similar media. After 3 days growth in passage 2, subcultures were made for passage 3. After 5 days growth subcultures were made for passage 4. Dry weights were determined for passages 3 and 4 after 5 days incubation.

Pythiomorpha failed to grow in the basal solution, but both *Aspergillus* and *Phycomyces* grew quite satisfactorily in that medium through the 4 passages. The addition of the mixture of mineral supplements nearly doubled the growth of *Aspergillus*, made the difference between no growth and

substantial growth for *Pythiomorpha*, and had relatively little effect on *Phycomyces*. Supplementing the basal solution with manganese materially improved the growth of *Aspergillus*, but was not nearly so effective as the complete mixture of supplements; for *Phycomyces* the addition of manganese had relatively little effect; for *Pythiomorpha* manganese was as effective as or more effective than the complete mixture.

DISCUSSION

In considering these results it should be remembered that our basal culture solution contained small amounts of manganese as well as other trace elements. The glassware was Pyrex, not quartz; the distilled water, while of good quality, was not redistilled; the chemicals were not purified by recrystallization or treatment with calcium carbonate. We were not concerned with the absolute necessity of any of the supplemental mineral elements for any of the fungi, but with the question: Why did *P. gonapodyides* fail to grow in a medium in which good growth of *Phycomyces* and *Aspergillus* occurred? It is evident that a deficiency of manganese in the medium was responsible for this result; the quantity of manganese in the basal solution was adequate for *Phycomyces* and *Aspergillus*, but not for *Pythiomorpha*.

Why should *P. gonapodyides* be so much more sensitive to a deficiency of manganese than *Phycomyces* or *Aspergillus*? Several possibilities may be suggested, for none of which we have direct evidence. The difference may be associated with a greater fixation of manganese in an unavailable form by the mycelium of *Pythiomorpha* than by that of either of the other two fungi. Such a situation might require more manganese to saturate the fixation system and supply that needed in metabolism. On the other hand, it is possible that the character of the metabolism differs in the three fungi to such an extent that more manganese is actually needed by *Pythiomorpha* than by *Aspergillus* or *Phycomyces*. The difference would not seem to be related to the solubility or insolubility of manganese in the culture medium. Our basal medium had an initial pH of between 4.5 and 4.7. Both *Aspergillus niger* and *Phycomyces blakeslecanus* increased the acidity of the medium by their growth. *Pythiomorpha*, however, had little effect upon the reaction of the nutrient solution as shown by determinations of the hydrogen-ion concentration in cultures 2, 3, 5, and 7 days old.

Another question which deserves consideration is why the amount of growth of *Pythiomorpha* should change in successive passages in the same supplemented medium. As a rule a marked increase was observed for the first three and sometimes four passages. The differences in the dry weights of *Pythiomorpha* in successive passages were not the result of minor differences in the composition of the solutions used, because all culture media for the successive passages in a particular experiment were aliquots of a

single solution prepared and autoclaved at the beginning of an experiment. A comparable situation was not observed with *Phycomyces* or *Aspergillus*. We assume that by continued cultivation of *Pythiomorpha* in a suitable solution a situation could be reached where the growth would be constant in successive passages; but judging from our results, this would require more than four passages. We might suggest that the phenomenon is associated in some way with the vigor of the inoculum. If so, it would seem further to be related most probably to differences in the activity of one or more enzyme systems, perhaps those with which manganese is associated. This possibility is suggested because the minuteness of the inoculum (a fraction of a milligram in dry weight) from which each culture starts would seem to require the intervention of some catalytic process to produce such differences in dry weight in successive passages as those noted (tables 2, 3).

The inactivity of zinc when used alone, and its beneficial effect in the presence of manganese, is of interest also. This suggests that these two elements play distinct roles in metabolism, a conclusion which follows also from the observations of other investigators that manganese cannot be replaced by zinc. It suggests also that the function in which zinc is active cannot occur until that in which manganese plays its part takes place.

In any event our results show that it is not possible to generalize from the requirements for mineral supplements of one fungus and apply the generalization too closely to others.

SUMMARY

The failure of *Pythiomorpha gonapodyides* to grow in a basal solution composed of magnesium sulfate, potassium dihydrogen phosphate, asparagine, and dextrose of C.P. grade plus synthetic thiamine was due to a lack of manganese. *Phycomyces blakesleanus* and *Aspergillus niger* grew quite satisfactorily through four successive passages in the basal medium. The addition of zinc and iron, singly or together, to the basal medium did not induce growth in *Pythiomorpha*. Zinc was beneficial in the presence of manganese.

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THE BEHAVIOR OF EXCISED ROOTS OF HETEROTIC HYBRIDS AND THEIR INBRED PARENTS IN CULTURE

W. GORDON WHALEY AND ALICE L. LONG

In 1941 a series of experiments was begun to study early growth behavior of certain hybrid and inbred strains of tomato and maize. Previous investigations by Ashby (1930, 1932, 1937), Murdoch (1940) and Whaley (1939) had indicated that much could be learned about the phenomenon of heterosis by investigating early post-embryonic growth. In this connection it was thought that cultures of excised roots would be of value since in the first passages they may be expected to show the influence of nutrient materials stored in the seed, and later they present a relatively uncomplicated growth system in conditions that can readily be controlled. Accordingly two sets of cultures were begun, one of tomato and one of maize. Since the techniques employed differed somewhat the data are here presented separately.

TOMATO

The tomatoes used were inbred lines of *Lycopersicon esculentum* kindly furnished by Mrs. Iva M. Burgess of the Maine Agricultural Experiment Station at Orono, Maine. One parent is designated as Red River, the other as Pritchard. Mrs. Burgess (1941) reported considerable hybrid vigor in crosses between these two lines and tests by the authors confirmed her findings. The seeds were sterilized by covering them with 95 per cent alcohol, transferring immediately to a 1 per cent solution of bichloride of mercury for one minute, and then rinsing in several changes of sterile water. It is probable that this treatment was too severe, since it was much less satisfactory than the azo-saline one reported by Robbins (1941). However, enough seeds germinated for purposes of the experiment. Germination was obtained by placing the seeds on a sterile 1 per cent plain agar. The F_1 seeds germinated most rapidly and their roots grew fastest. By proper timing it was possible to obtain the inocula from roots of approximately the same length. Five-millimeter terminal segments were cut with a sterile surgical scalpel from roots about 10 mm. in length. These were transferred to culture flasks. The basal nutrient solution contained per liter 0.333 g. $\text{Ca}(\text{NO}_3)_2$; 0.063 g. $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$; 0.063 g. KNO_3 ; 0.042 g. KC_1 ; 0.060 g. KH_2PO_4 ; and 0.0025 g. $\text{Fe}_2(\text{SO}_4)_3$. All culture solutions contained 2 per cent C.P. cane sugar. For the first passages 0.001 g. of thiamine per liter was added.

TABLE 1. *Average dry weights (mg.) of excised tomato roots grown in solutions supplemented with thiamine.*

Average of 5 roots. Growth period of 45 days for each passage.

	Passage			
	1	2	3	4
Red River	1.3	2.3	2.2	2.6
Pritchard	1.4	1.9	2.0	2.5
F ₁	3.3	4.2	4.9	5.4

The roots were grown in 50 ml. of solution in 125-ml. Erlenmeyer flasks kept in diffuse light at 20°–25° C. Sub-cultures were made at 45-day intervals and at the same time each root system (minus a five-millimeter terminal piece removed as inoculum) was carefully washed and dried at 100° C to furnish an index of growth. The amounts of growth attained by each of the lines in the first four passages are given in table 1.

As in the data presented by Robbins (1941) for a cross between Red Current (*Lycopersicon pimpinellifolium*) and Johannesfeuer (*L. esculentum*), the roots of the F₁ which showed hybrid vigor in general vegetative characters, grew consistently more rapidly in the cultures. The increase in growth during successive passages was probably at least partly due to temperature differences. All cultures were within the 5° C range but later passages were grown at the upper end of the range. There may also have been an adjustment period which reduced growth somewhat during the first passage.

At the end of the fourth passage segments were transferred to solutions containing in addition to the thiamine 0.001 g. of pyridoxine and 0.005 g. of nicotinamide per liter. This final transfer was made in two different ways. Those roots designated as Set I in table 2 were subcultured as outlined

TABLE 2. *Average dry weights (mg.) of excised tomato roots grown in solutions supplemented with thiamine, thiamine and pyridoxine, and thiamine, pyridoxine and nicotinamide.*

Growth period 45 days; 5th passage. Average of 5 roots.

	Thiamine	Thiamine Pyridoxine	Thiamine Pyridoxine Nicotinamide
<i>Set I</i>			
Red River	2.9	3.1	5.1
Pritchard	2.6	4.2	4.8
F ₁	6.2	10.8	17.4
<i>Set II</i>			
Red River	3.1	3.4	4.9
Pritchard	2.2	5.1	5.6
F ₁	6.8	12.7	19.1

above from different roots of the same stock, i.e., each root came from a different seed. Those designated as Set II were obtained by taking the apical segments of the main and lateral branches of the same root. Set II represents root clones while Set I represents different roots of the same genetic stock. Unfortunately the small number of roots used did not permit reliable determination of differences in amount of variation between these two sets.

In both sets the two parents and the hybrid grew better with thiamine and pyridoxine, and still better with thiamine, pyridoxine, and nicotinamide than with thiamine alone. All the hybrid roots grew much more rapidly than those of the inbred parents. Even from so limited an experiment it is possible to draw some conclusions regarding the effects of the different growth substances on the inbred and hybrid lines. Robbins (1941) made a good critical analysis of this question based upon his more extensive data. He found that the roots of one parent (Johannesfeuer) showed a greater response to pyridoxine than those of the other (Red Currant). The roots of Red Currant showed a greater response to nicotinamide than those of Johannesfeuer. The present data seem to suggest that the roots of Pritchard respond better to pyridoxine while those of Red River respond better to nicotinamide. In connection with the fact that the differences here are less distinct than those in Robbins' data it should perhaps be remembered that the two inbred parents in this case are members of the same species, and hence, presumably less genetically different than a line of *L. esculentum* and one of *L. pimpinellifolium*. Robbins found further that when grown in solutions supplemented by all three growth substances one parent (Red Currant) tended to approach the hybrid in amount of growth. In the present experiments neither parent showed an approach to the hybrid with any of the growth-substance supplements used. It is notable in fact, that with thiamine, pyridoxine, and nicotinamide growth of the hybrid roots was increased to almost three times what it was with thiamine alone, while that of each parent was only about twice as great. These data furnish some evidence for Robbins' idea that one of the factors concerned in heterosis may be the ability to synthesize or utilize certain growth substances and that hybrid superiority may be partly due in some instances to ability derived from one parent to synthesize or utilize to better advantage one group of essential substances, and from the other parent ability to synthesize or utilize a different set of essential substances.

MAIZE

Although it was recognized that maize roots are apparently not adapted to comparatively easy culture by the methods so far evolved, as are those of tomato, it was thought that an attempt to culture them might reveal

some data of interest. After several abortive essays a partially successful method was developed. The data contribute nothing toward the solution of how to grow maize roots in culture but they do seem to have some significance for certain aspects of the heterosis problem.

Seeds were sterilized by soaking for two minutes in 95 per cent alcohol and then transferring to a 2 per cent solution of bichloride of mercury for two minutes. The seeds were then washed thoroughly in four changes of sterile water and germinated on moist filter paper in sterile Petri dishes. The roots were allowed to grow until a 10-millimeter segment could be cut from the apex for transfer to the culture solution. It was found that in

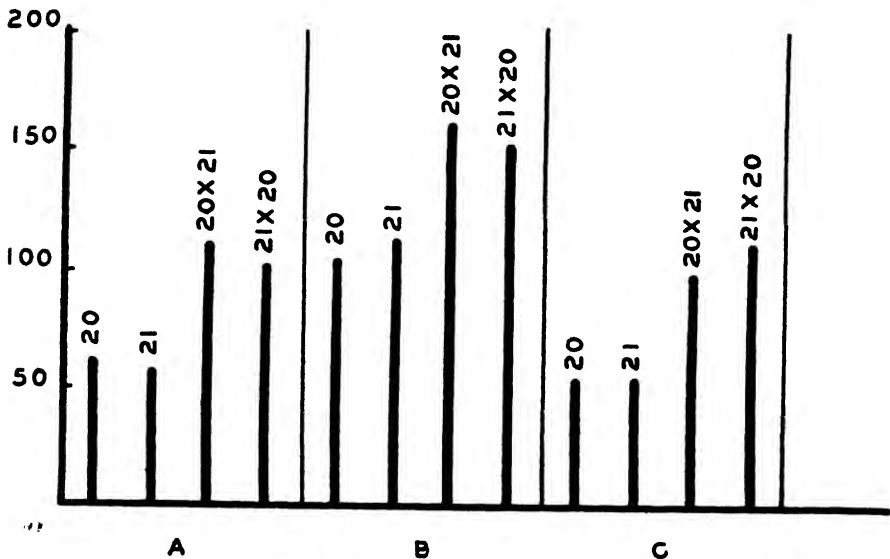


FIG. 1. Average growth (length) of maize roots (lines 20, 21, and hybrids) in solutions supplemented with (A) thiamine, (B) thiamine and pyridoxine, and (C) thiamine, pyridoxine, and nicotinamide. Average of the first six passages, each passage of seven days; average of ten roots per passage.

both crosses used the hybrid seeds germinated much more rapidly. To compensate for this growth difference and for individual variation from seed to seed within a strain, large numbers of seeds were started at predetermined intervals. In this way 10-millimeter segments were all cut from roots of approximately the same length. Eighteen cultures of each strain were started, but measurements were made on only ten; the ten showing greatest growth being selected in each instance. Various basal media were tested, Pfeffer's solution, which was also used in culturing the tomato roots, finally being chosen. Instead of sucrose all solutions contained 1.6 per cent dextrose and were made semi-solid by addition of 5 g. purified agar per liter. (Purification of agar was by the pyridine-ethyl alcohol method out-

lined by Robbins and Ma, 1941.) Growth conditions were the same as those noted above. Subcultures were made at seven-day intervals since it was found that subculturing at frequent intervals resulted in better growth of all the roots. Since roots of the strains used are approximately the same in diameter and since no secondary roots were developed, length was chosen as the simplest measure of growth. Seeds of two crosses were obtained from Dr. D. F. Jones of the Connecticut Agricultural Experiment Station at

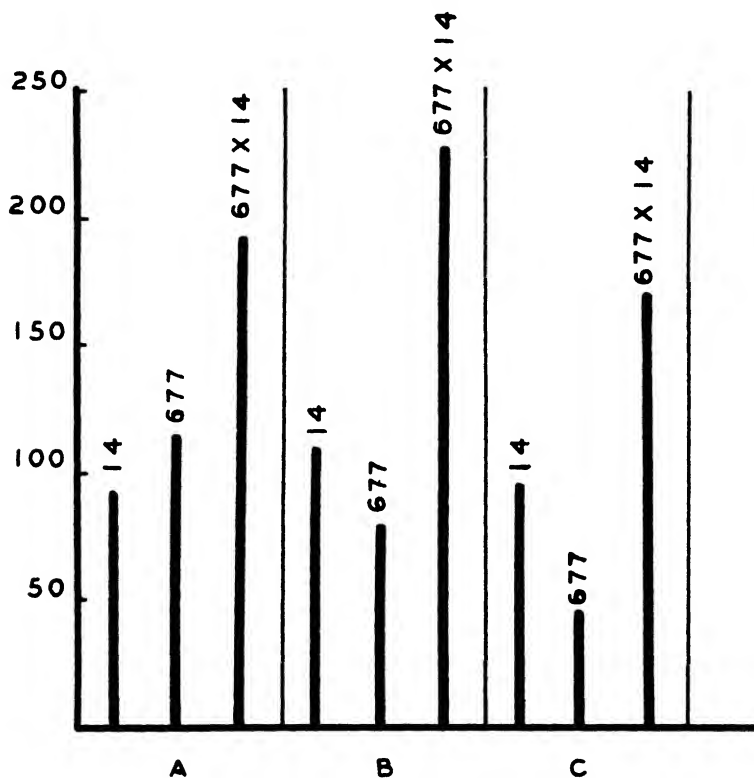


FIG. 2. Average growth (length) of maize roots (lines 14, 677, and hybrids) in solutions supplemented with (A) thiamine, (B) thiamine and pyridoxine, and (C) thiamine, pyridoxine, and nicotinamide. Average of the first six passages, each passage of seven days; average of ten roots per passage.

New Haven. The inbreds and crosses are designated as 20, 21, 20×21 , 21×20 , and 677, 14 and 677×14 , respectively. These crosses showed considerable hybrid vigor under both field and greenhouse conditions.

With these roots culture solutions were augmented from the beginning with thiamine, thiamine and pyridoxine, or thiamine, pyridoxine, and nicotinamide in the amounts of 0.001 g., 0.001 g., and 0.005 g. per liter, respectively. Figures 1 and 2 show average growth of ten roots of each type during the first six passages. To those roots whose growth is repre-

sented in block A thiamine was added; to group B thiamine and pyridoxine; to group C thiamine, pyridoxine, and nicotinamide. In the 20, 21 material the addition of pyridoxine to cultures already containing thiamine caused a marked growth increase in roots of both hybrids and inbreds. This increase appeared to be absolutely, and not relatively, about the same in all strains. The condition would seem to indicate a pyridoxine deficiency in both parental strains and their hybrids. The addition of nicotinamide, in the concentration used, to cultures containing both thiamine and pyridoxine brought about a marked reduction in root growth as compared with that in cultures containing thiamine and pyridoxine. The amount of growth in

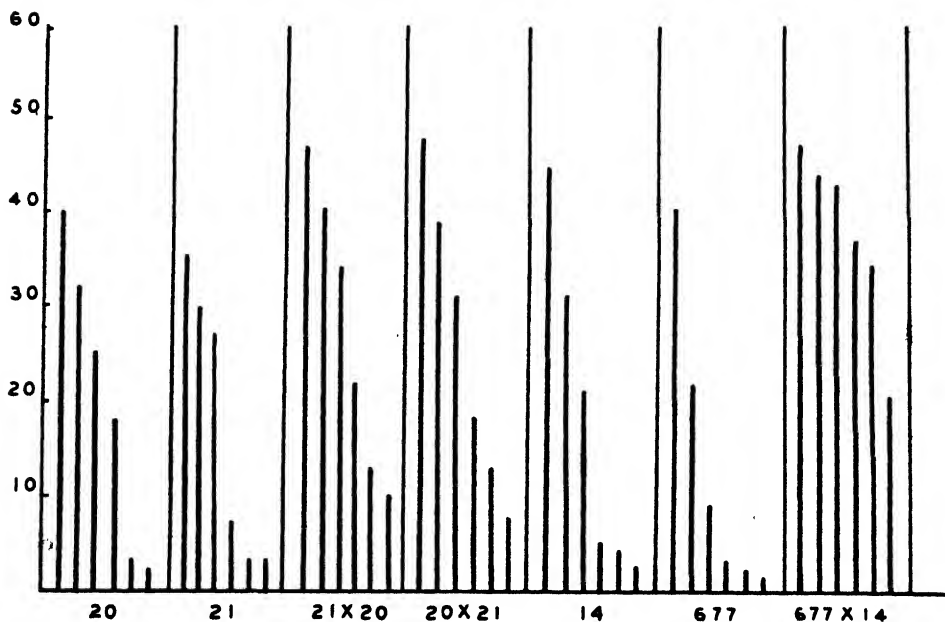


FIG. 3. Average growth (length) of maize roots during each of the first six passages. Average of ten roots in each passage; passages of seven days each. Cultures supplemented with thiamine and pyridoxine.

cultures containing all three substances about equaled that in cultures containing thiamine alone. Further experimentation would be necessary to discover the reason for the inhibition of growth by nicotinamide.

The roots of lines 677 and 14, and the cross 677×14 reacted in a somewhat different manner. As in the above experiment the hybrid roots here consistently grew better than those of the inbreds. The actual hybrid advantage above either the average of the parents, or the better parent is higher in this case than in the preceding one. When cultures containing thiamine and pyridoxine were compared with those containing thiamine alone in this case it was seen that the growth of one parent (14) and the hybrid (677×14) was increased. The growth of the roots of the other

inbred (677) was decreased. The further addition of nicotinamide again had the effect of limiting growth, but not quite as uniformly as in the previous cross. One inbred (14) was decreased but little, its growth being still greater than with thiamine alone. The other inbred (677) was decreased very markedly, its growth being less than half that with thiamine alone. The hybrid was decreased by about the same amount as in the 20 × 21 cross.

The data seem to indicate that 14 and 677 × 14 are deficient in their ability to synthesize pyridoxine. The significance of the reaction of 677 is not suggested. This inbred line was difficult to handle in all the experiments. Germination was slow, and the percentage very low. Even the best cultures showed a tendency toward lateral branching characteristic of inhibited growth.

Figure 3 shows the average growth of ten roots of each line during each of the first six passages. These cultures were supplemented with thiamine and pyridoxine, since this combination generally gave the best growth. The inadequacy of the method is disclosed by the manner in which the growth diminished from one passage to the next. It is significant, nevertheless, that growth of the hybrid roots decreased to a lesser extent and less rapidly than that of the inbreds. The hybrid 677 × 14 was particularly outstanding in this respect. Roots of this plant made by far the most satisfactory growth. Of all the plants used only this one made satisfactory growth beyond the sixth passage.

DISCUSSION

The use of excised roots permits study of certain metabolic processes under conditions much less complex than those encountered with intact plants. The data presented here indicate that heterosis produces hybrid vigor in small portions of roots grown in culture media under laboratory conditions. This fact is revealing with respect to the physiological mechanism responsible for hybrid vigor. It allows elimination of some factors as being of primary importance in the production of hybrid vigor. Ashby's work (1930, 1932, 1937) indicated that photosynthesis played no part in the hybrid advantage in either maize or tomato. The present data certainly show that hybrid vigor is developed without photosynthesis. (Data to be published subsequently show that photosynthetic differences may increase the relative amount of hybrid vigor.) The gas exchange incident to photosynthesis, and the various translocation factors are also eliminated here. Ashby finally decided upon the size of the meristematic mass within the embryo as the immediate causal agent. He was primarily concerned with the stem apical meristem since this is the source of the bulk of plant tissues. In root cultures the only continuing meristematic mass is the root meristem.

Histological examination of the root tips in the present study revealed no size differences among the different root meristems. The "meristematic mass" influence is therefore ruled out in this case. Nutrient materials derived from the seed are also ruled out for quantitative considerations. The original apical segments were cut from the roots before the available nutrient material in the seeds was exhausted. In intact plants the hybrid might gain an advantage by a longer endosperm nutrition period during the early seedling stage. In the tomato and maize strains tested, hybrid vigor cannot be directly dependent upon this factor. There still remains the possibility of qualitative influence of seed-stored nutrient materials. Certain substances might be more readily available to the hybrid embryos, or be of greater potency. In tomato this seems a very remote possibility in relation to the better growth of the roots in culture. Each root segment was allowed to grow for 45 days before subculturing. In the fifth passage, 180 days from germination of the seed, the roots were still making relatively the same amount of growth as in the first passage. Seemingly any advantage arising from qualitative differences in seed nutrients would have disappeared long before this point was reached. The behavior of the corn roots in culture makes an evaluation of this factor more difficult. The diminution of growth in progressive passages might suggest that some essential substance is derived from the endosperm, and that the original amount diminishes in each passage. That the continued advantage of the hybrids during successive passages depended altogether upon greater availability of this substance seems again unlikely.

The data are best interpreted on the assumption of fundamental metabolic differences between the inbreds and hybrids. In the tomatoes, roots of Pritchard were unable to synthesize pyridoxine in amounts sufficient to permit maximum growth. The roots of Red River had a like deficiency with respect to nicotinamide. Crossing produced hybrids in which the deficiencies of both parents were largely eliminated. The simplest genetic interpretation of this situation is that each parent is homozygous for a deleterious recessive factor—the inability to synthesize, or utilize enough of a certain substance or substances. These recessives appear to be at different loci in each parent since crossing masks their effects. This explanation may hold only for the experimental conditions maintained, but that does not affect its validity. Much the same interpretation may be made for the corn root cultures. Here, however, certain of the substances utilized to greater advantage by the hybrid may be derived from within the system, perhaps from the endosperm instead of from the culture media. An exhaustion of such substances may partially account for the progressive diminution of growth in successive passages. It is probable that fundamental physiological differences are to be expected between two such plants.

The differences between the excised hybrid and inbred roots appear then to be fundamental differences in cellular metabolism. These differences in the efficiency of metabolism appear to depend partly, in turn, upon the supply, either internal or external, of certain essential substances.

SUMMARY

Excised roots of tomato and maize were grown in Pfeffer's solution containing separately thiamine; thiamine and pyridoxine; and thiamine, pyridoxine, and nicotinamide. In cultures containing thiamine the roots of one inbred strain of tomato, Pritchard, responded better to the addition of pyridoxine. Those of the other, Red River, responded better to the addition of nicotinamide. The hybrid roots were better than those of either inbred in all culture media.

Excised maize roots showed progressive growth diminution in successive passages in all media. The hybrids showed greater growth in each of six passages, and greater average growth than the inbreds. In cultures containing thiamine the parents and hybrids of one cross, 20, 21, 20 \times 21, and 21 \times 20, showed increased growth in the presence of pyridoxine, decreased growth in the presence of pyridoxine and nicotinamide in the concentration used. The roots of the other cross reacted in a like manner but less consistently.

It is suggested that the hybrid advantage derived from more efficient metabolism giving the hybrid roots greater ability to synthesize and/or utilize certain essential substances.

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FLORAL ANATOMY OF SOME SPECIES OF CORNUS

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INTRODUCTION

This investigation of the genus *Cornus* is part of a study of members of the Cornaceae, Araliaceae, Caprifoliaceae, and Rubiaceae. The purpose of the study is to discover, if possible, evidence indicative of the fundamental structure of the inferior ovary, and the relation of these families to one another and to other families.

A review of the extensive literature on the nature of the inferior ovary by Miss Gertrude Douglas (6) has appeared in a recent number of the Botanical Review. This literature is also discussed, in part, in MacDaniels' paper (10) on the structure of various pome fruits. However, with respect to the morphology of the Cornaceae, publications are meager and have come primarily from the work of Horne (8), Martel (11), and Baillon (1). These publications will be considered in the discussion.

MATERIAL AND PROCEDURE

So far as possible, living material of buds, flowers, and young fruits was used in the preparation of slides.

Fresh material was killed and fixed in F.A.A. made up with 70 per cent ethyl alcohol (3). After having been washed with 70 per cent ethyl alcohol, the material was placed first in 83 per cent, then in 95 per cent ethyl alcohol. Dehydration was completed by successive immersions for an hour in each of the following mixtures:

95 per cent ethyl alcohol	3 parts	1 part	1 part
Tertiary butyl alcohol	1 part	1 part	3 parts

Several changes in pure tertiary butyl alcohol followed, before the material was gradually infiltrated with paraffin.

Herbarium material was first softened in a solution of 1 per cent NaOH or KOH for 12-24 hours, then washed in running water 12 hours. Dilutions of ethyl alcohol were used to dehydrate, after which dehydration and infiltration proceeded as above.

A rotary microtome was used for sectioning and the sections mounted serially. Miss Jackson's crystal-violet-erythrosin schedule (9) was used with slight modifications. In staining herbarium material, a mordant was necessary to secure adequate differentiation. Before being stained in crystal violet, therefore, the slides were placed in a 1 per cent aqueous solution of chromic acid.

No less than three and an average of five serials of each species, were examined. Because of the anatomical variability found, the actual number of flowers of each species is of interest; these numbers are as follows:

<i>C. florida</i> 4	<i>C. brachypoda</i> 4
<i>C. mas</i> 5	<i>C. glabrata</i> 3
<i>C. canadensis</i> 4	<i>C. racemosa</i> 4
<i>C. suecica</i> 9	<i>C. stricta</i> 4
<i>C. controversa</i> 5	<i>C. alsophila</i> 5
<i>C. alternifolia</i> 5	<i>C. rugosa</i> 5
<i>C. oblonga</i> 3	<i>C. Amomum</i> 5
<i>C. Drummondii</i> 5	<i>C. stolonifera</i> 8

In all, sixteen species of the genus were sectioned and studied. These comprise a third of the genus, and were selected to represent as many subgroups in the genus as possible. Herbarium sheets of the species are cited.

GENERALIZED FLORAL ANATOMY

In gross morphology, the flower of *Cornus* is 4-merous, generally perfect, and epigynous. The bilocular ovary has a single style, and, pendant from the upper part of the septum, a single anatropous ovule in each locule.

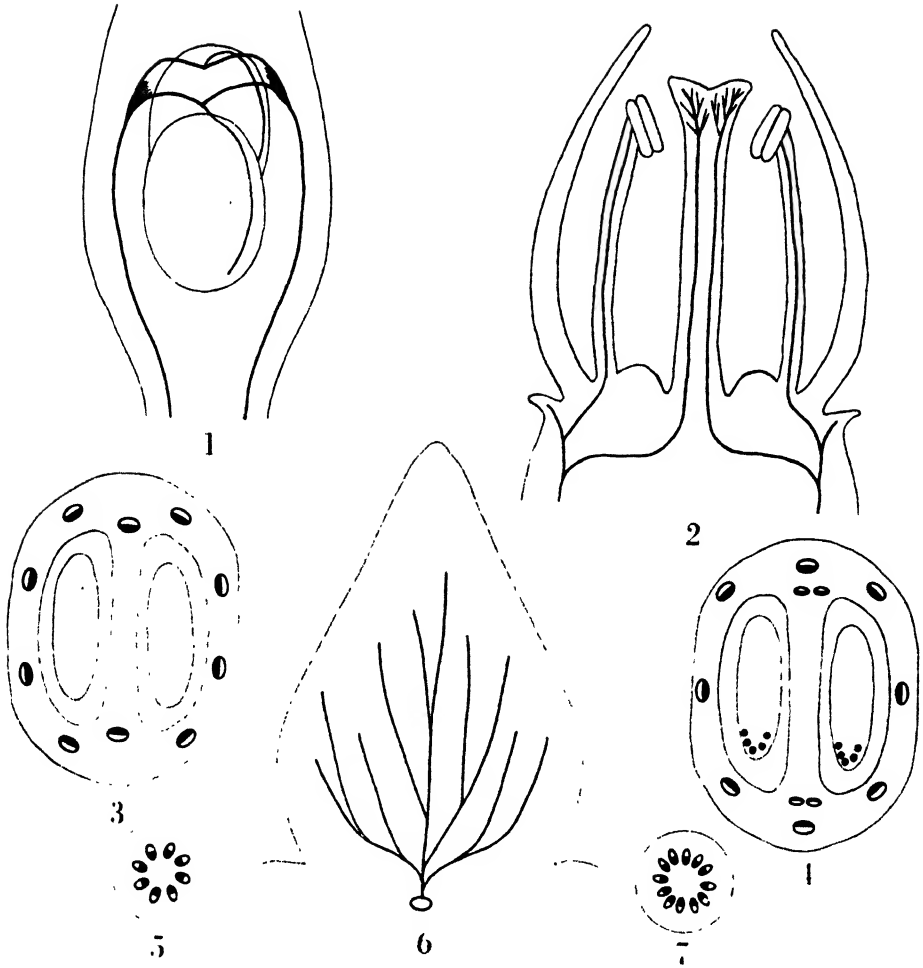
Although the floral anatomy indicates that the essential structure of certain gross features is different from the apparent structure, it does in general substantiate the gross morphology. To minimize repetition, and to establish a basic pattern for the description of the individual species, the floral anatomy of a generalized type is first described. This generalized flower type is characteristic of no particular species, nor is any anatomical feature described necessarily common to all the species studied.

Beginning at the lower part of the receptacle, the vascular tissue is found to consist of a ring of several bundles.¹ These become organized into eight main bundles (fig. 5) which gradually and simultaneously proceed toward the periphery. Usually in the receptacle, but occasionally in the ovary proper, a ventral bundle separates centripetally from each of two opposite bundles. This bundle is composed of a ventral trace of one carpel and the adjacent ventral trace of the second carpel. These always run up in the wall of the ovary, at each end of the septum (fig. 3). Before reaching the region of ovular attachment, the ventral bundles fork radially (fig. 4) and, somewhat above this region, divide into several traces which form an arc

¹ The term bundle is here used in two senses: to mean a vascular cord morphologically composed of several traces, or the strand within the floral member. A trace is the vascular strand supplying an organ from its place of origin (often receptacle) to its entrance into that organ. To illustrate: the ovular bundle is the vascular supply within the ovule; the ovular trace is the vascular strand which runs from the ovule to the ventral bundle; the ventral bundle consists of two ventral traces which are morphologically distinct but often fused and histologically inseparable. See Eames (7) for terminology.

running periclinally in the ovary wall (fig. 13). The outer traces arch and descend in the septum to the region of the funiculus, where each unites with the opposite trace of the corresponding carpel. The bundle resulting from the union enters the ovule (fig. 1). All but one or two of the intermediate branches also arch and descend toward the septum but terminate at various levels and at various distances from the ovary wall (fig. 1). The exceptional traces unite and turn in toward the center, where they enter the style and end in the lower half of the stylar column (not shown in figure 1). Within the ovule, the ovular bundle descends the length of the raphe, branching distally. In the upper part of the ovary, sometimes even above the locule, the dorsal traces separate from two opposite peripheral bundles of the ovary (fig. 2). When they reach the top of the ovary, they extend horizontally toward the style and enter it, continuing to the stigma and branching profusely (fig. 2). In the lower half of the ovary, lateral traces of the carpel separate from the peripheral bundles. These proceed various distances up the ovary wall. Most of them bend centripetally at the top of the ovary and run horizontally: some of these end free; others join the dorsal traces.

The eight main bundles remaining are the peripheral bundles. In the body of the ovary, these have a definite arrangement with respect to the ventral bundles. The bundles with which the ventral bundles are united at the base may still be more or less in the same radii as the ventral bundles (fig. 4); or they may shift periclinally in opposite directions so that they lie in the line of the locule (fig. 3). In either case, the remaining six bundles are accordingly disposed in radial symmetry. Since the change is secondary, and since the arrangement is not constant for a species, it seems of slight importance. Of the eight bundles, four are stamen bundles and the alternating four are petal bundles. Each stamen bundle divides tangentially. Of the two resulting traces, the centrifugal trace is the sepal trace; the centripetal, the stamen trace (fig. 26). The petal bundles, however, divide radially, cutting off a small trace on each side (fig. 26). The middle trace is the petal trace, and each of the lateral traces is a lateral trace of the sepal adjacent. The sepal supply, therefore, consists of the trace centrifugal to the stamen trace, plus the adjacent traces separated radially from the petal bundle on each side of the stamen bundle. In close succession, the sepal traces enter the sepals; the petal traces, the petals; and the stamen traces, the stamens. Within the sepal, the median trace is the strongest, the lateral traces being weak and scarcely entering the calyx lobe. Within the petal, the petal trace forks several times, resulting in a highly vascularized petal (fig. 6). The stamen bundle usually continues single in the filament. Above the departure of the traces to the various floral cycles is a mound-like nectariferous disc which consists of deeply-staining secretory cells (fig. 2). The disc, however, has no vascular supply.



FIGS. 1-7. *Cornus*: Anatomy of the flower. FIG. 1. Ovular and ventral supplies. Ventral traces not bending centripetally in the receptacle; ovular traces arching in the septum, uniting with the opposite ovular trace of the same carpel; intermediate (vestigial) ovular traces also arching but ending in the septum. FIG. 2. Sepal, stamen and dorsal trace derived from a peripheral bundle of the ovary; distal branching of the dorsal bundles in the stigma; mound-like nectariferous disc above the ovary without vascular supply. FIG. 3. Ventral bundle composed of ventral trace of one carpel and the adjacent ventral trace of the second carpel; the ventral bundles are located in the ovary wall at each end of the septum; peripheral bundles with which the ventral bundles are united at the base are not in the same plane as the ventral bundles at this higher level. FIG. 4. Pair of "foreign" ventral traces in the ovary wall at each end of the septum; pair of peripheral bundles with which ventral traces are united at the base are in the same plane as the ventral traces at this higher level—this contrasts with the condition in fig. 3; branching of ovular bundle in the ovule. FIG. 5. Eight main bundles in the receptacle. FIG. 6. Branching of the petal bundle after entering the petal. FIG. 7. *C. florida*. Stele of the receptacle differing from the condition in other species studied (fig. 5), in having numerous strands.

ANATOMICAL DESCRIPTION OF SPECIES

A description of the anatomy of each species follows. If the anatomy resembles that of the generalized flower type, it is omitted.

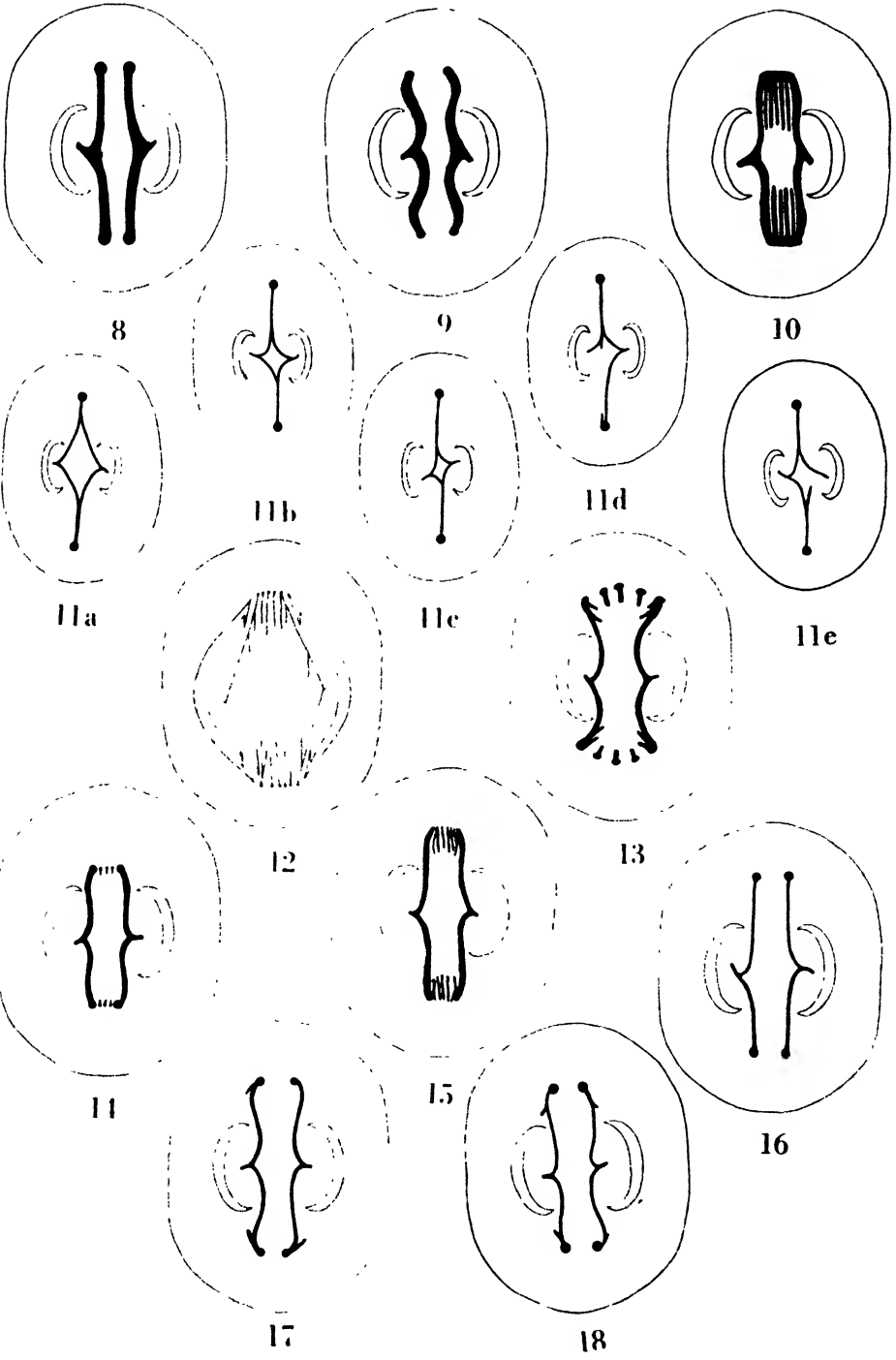
1. *C. FLORIDA* L. A. *Miele* 283 (C).

The receptacle of this species differs from that of the rest of the species studied in having a stele composed of numerous instead of several strands (fig. 7). Nevertheless, as in the other species, these become organized as eight bundles. In some specimens, the ventral bundles are cut off from the stamen bundle, in others from the petal bundle. From its origin, the ventral bundle continues fused to the region of ovular attachment, where it divides into its two component traces. Very shortly, each ventral trace bends inward and becomes an ovular trace to the ovule of its respective carpel. The ovular trace is an extraordinarily heavy one and it arches only slightly, extending almost horizontally in the septum (fig. 8). The fusion of the ovular traces of the same carpel before entering the ovule is very light, for the identity of the pair is apparent as they swing across the top of the ovule. Though the ventral traces usually terminate in the ovular traces, two specimens show a ventral trace continuing beyond the roof of the locule. Here the ventral bundle divides into three: two outer heavy strands, the ovular traces; and a slender middle strand, the ventral trace. In flowers with the ventral bundles associated with the sepals, the dorsal traces arise from the alternate sepal bundles; where the ventrals are associated with petal bundles, the dorsal traces arise from the remaining two petal bundles. In one flower, the dorsal trace of one carpel separates from the petal bundle, the dorsal trace of the other carpel from the sepal bundle. There are no lateral traces in this species. The sepal supply is the most extensive and complex of all the species studied. The bases of the sepals are united into a tube almost 1 mm. long. This is one-third the length of the calyx and is the most extensive fusion found. From both stamen and petal bundles, two traces are cut off radio-tangentially. These traces divide usually twice and the branches ascend in the calyx tube and anastomose somewhat (fig. 21). The species is rather conspicuous in the precocious division of the sepal and stamen bundles. This cleavage often occurs at a level below the roof of the locule; in two stamen bundles the separation occurs half-way down the ovary. The petal supply stands in strong contrast to the sepal supply in having the single petal trace divide into just three branches after entering the petal.

2. *C. MAS* L. A. *Miele* 281 (C).

This species is somewhat intermediate between the preceding species and the pair of "herbaceous" species to follow.

The ventral bundles usually separate rather high in the ovary from the stamen bundle. Though two flowers show one ventral bundle double and



one single, the usual condition is a fusion of the two unrelated ventral traces more than half the length of the ovary. After forking, the pair of ventral traces move apart in their ascent. When they reach the region of ovule attachment, they turn into the septum, without arching (fig. 9). As in *C. florida*, the ovular traces are very heavy (fig. 9). The ovular bundle does not branch. Surrounding each locule is a ring of large secretory cells (fig. 36). The dorsal traces are weakly differentiated and arise from the petal bundles or stamen bundles according as the ventrals arise from these. Weak differentiation of a few other bundles in one ovary makes it difficult to ascertain whether they are ramifications of the dorsal trace, or weak lateral traces. The sepal supply of this species is not so complex as that of *C. florida*. The petal bundles behave like those of the generalized flower type. The stamen bundles, however, divide tangentially to produce either three separate strands or one strand with two lateral branches close to the base. Each of these lateral branches runs periclinally in the ovary and unites with the adjacent sepal trace of the nearby petal bundle (fig. 23).

Within the petal, the petal trace may remain single or divide to form three strands.

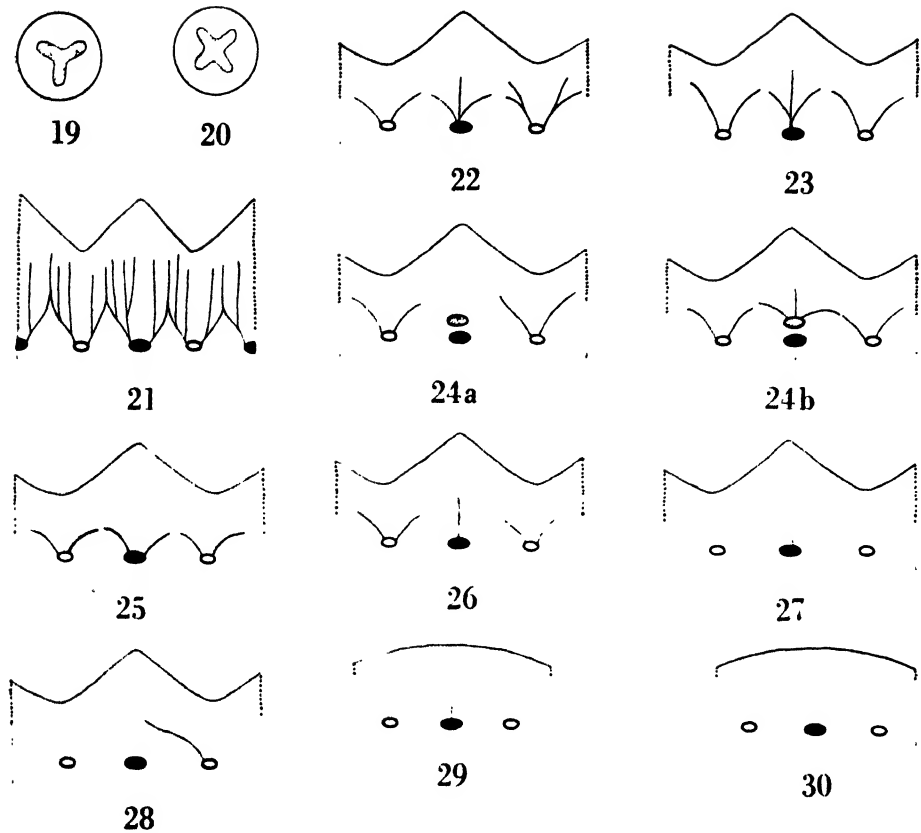
One flower was found to be tricarpeal. It differs from the bicarpeal flowers only in having three ventral bundles and three dorsal traces.

3. *C. CANADENSIS* L. A. Miele 285 (C).

The ventral traces, usually separate for the greater part of their length, separate from the stamen bundles relatively high in the ovary—usually near the base of the locule and in one flower in the upper fourth of the ovary. As in the two preceding species the ventral traces terminate in the ovular traces. About level with the roof of the locule, these bundles arch and descend through the septum, each uniting with the corresponding ovular traces

Explanation of figures 8-18

Variations in the ovular supply as seen in X-sections of the ovary. In these diagrams, the arching indicated in fig. 1 is telescoped onto one plane. FIG. 8. *C. florida*. Heavy, scarcely arching ovular traces. FIG. 9. *C. mas.* Heavy, slightly arching ovular traces. FIG. 10. *C. canadensis*. Ventral traces terminate in the ovular traces. (Vestigial ovular traces are drawn here for clarity and convenience); ovular traces heavy. FIG. 11a-c. *C. suecica*. a-c, stages found in different specimens showing the fusion of the pair of ovular traces supplying separate ovules. d, ovule supplied by ovular trace from one side of the carpel only, the corresponding ovular trace not reaching into the septum; one ovular trace gives indication of branching. e, as in 11d, but all of the traces enter the septum. FIG. 12. *C. controversa*. Light ovular traces which branch; vestigial ovular traces. FIG. 13. *C. brachypoda*, *C. rugosa*. Periclinal arc of bundles in the wall of the ovary; branching of the ovular traces; vestigial ovular traces. FIG. 14. *C. racemosa*. Heavy ovular traces; small vestigial ovular traces; narrow arc of bundles. FIG. 15. *C. alsophila*. Heavy ovular traces; vestigial ovular traces; arc of bundles. FIG. 16. *C. stolonifera*. Light ovular traces. FIG. 17. *C. stolonifera*. Branching of ovular traces. FIG. 18. *C. stricta*. Light ovular traces which branch.



FIGS. 19, 20. Types of styler canals. FIG. 19. 3-lobed styler canal. FIG. 20. 4-lobed styler canal. FIGS. 21-30. Types of sepals and sepal supplies. The heavy stippling of the cuts indicates the extent of the calyx; the light stippling, the ovary proper. Outline bundles are petal bundles; solid black bundles are stamen bundles or traces; stippled bundles are sepal traces. In figs. 22-25, the union of the sepal traces derived from the stamen bundles and the adjacent petal bundles is not indicated since it is for so short a distance, and the sepal traces themselves quite short. FIG. 21. *C. florida*. Relatively long calyx tube; sepal traces cut off radio-tangentially from the stamen and petal bundles; sepal traces branching freely and anastomosing in the calyx tube. FIG. 22. *C. Drummondii*. Sepal traces derived from both stamen and petal bundles; both branching. FIG. 23. *C. mas*, *C. glabrata*, *C. brachypoda*. Sepal traces derived from the stamen and petal bundles, the trace from the stamen bundle branching. FIG. 24a, b. *C. stricta*, a, single sepal trace from stamen bundle, two sepal traces from petal bundle. b, branching of the sepal trace derived from the stamen bundle. FIG. 25. *C. racemosa*. Two unbranched sepal traces from stamen and petal bundles. FIG. 26. *C. Amomum*. Typical 3-traced sepal—middle trace cut off centrifugally from stamen bundle; two sepal traces cut off radially from petal bundle. FIG. 27. *C. canadensis*, *C. stolonifera*, *C. suecica*. Sepal trace only from stamen bundle and this unbranched. FIG. 28. *C. suecica*. Sepal trace from one of petal bundles adjacent to sepal; no sepal trace from the stamen bundle. FIG. 29. *C. controversa*, *C. stolonifera*. Single sepal trace derived from stamen bundle, but terminating in the ovary wall. FIG. 30. *C. alternifolia*, *C. suecica*, *C. stolonifera*. No sepal traces cut off.

(fig. 10). As in *C. mas*, the ovular bundle remains single. At opposite sides of the upper part of each locule in a line parallel with the septum is a band of enlarged cells. Also in the upper part of the ovary, showing no constancy in the bundles with which they are associated, the dorsal traces appear. The single sepal trace, which passes through the microscopic calyx tube and ends in the base of the calyx tooth, is derived from the stamen bundles. In this species, the petal bundles do not give off sepal traces (fig. 27). The petal trace continues unbranched in the petal.

4. *C. SUECICA* L. *Fernald & Wiegand 5965* (C).

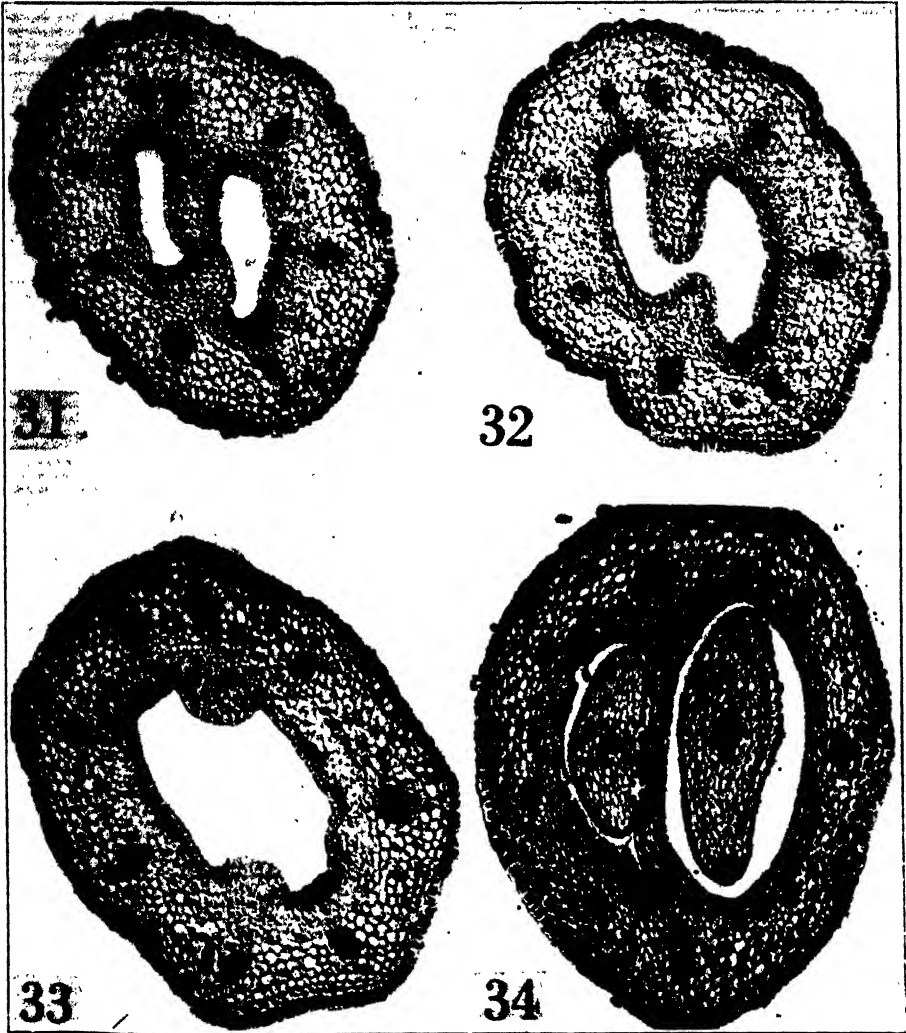
The ventral traces of *C. suecica*, except for their union through most of the length of the ovary, resemble the ventral traces of the preceding species. This species, moreover, displays the most extreme fusion of the ovular traces. In it, the "foreign" ovular traces (those of the two carpels) are fused almost to the center of the septum where they separate in joining their "sister" ovular traces (those of the same carpel) (figs. 11a-11c). In one extreme case, one ovular trace does not reach into the septum (fig. 11d); in another, the ovular trace extending into the septum fails even to turn toward its respective ovule (fig. 11e). As in *C. mas* and *C. canadensis*, the ovular bundle remains single. The dorsal traces usually arise from the petal bundles but a few seem to be derived from the stamen bundles. Though in half the flowers examined, the sepal supply is similar to that of *C. canadensis*, the condition in the other half shows interesting deviations from that of this species. In four flowers some (one, two, or three) petal bundles divide as well as the stamen bundles. Of these flowers, two have stamen bundles which do not divide. In the first such flower this is true of two stamen bundles, and the corresponding sepal either is without vascular tissue (fig. 30) or it derives its single trace from one of the adjacent petal bundles (fig. 28). In the second flower only one stamen bundle remains undivided. Here the supply to the corresponding sepal is again derived from the adjacent petal bundle (fig. 28).

This last flower differs in another respect from the other flowers of this genus. Its ovary lacks a septum. At the base of the ovary is a septum separating the two small locules (fig. 31). Shortly, however, the septum separates into two protuberances extending from the ovary wall into the locule (fig. 32). Each of these projections is covered by an epidermis continuous with that lining the ovary wall. These projections recede toward the ovary wall (fig. 33) and finally disappear so that in the upper half of the ovary there is no evidence of their presence below. There are no ventral bundles and no ovules in this ovary.

In this species, the petal supply does not differ from that of *C. canadensis*.

5. *C. CONTROVERSA* Hemsl. *Steward & Cheo 231* (NY).

This and the following species are the two alternate-leaved species in the genus. In this species, the ventral traces separate from the two opposite petal



FIGS. 31-33. *C. succica*. Cross section of the ovary at three successively higher levels showing incomplete septation of the ovary—the septum complete at the base, but receding acropetally toward the ovary wall. In fig. 32, the appearance is that of two parietal placentae. FIG. 34. *C. succica*. Cross section of ovary showing abortive carpel and ovule.

or stamen bundles, and behave as described in the generalized floral type. Both these species differ from the opposite-leaved species studied in the shape of the septum in the upper part of the ovary. Whereas in transverse

section the septum of other species is usually a band of tissue separating the two locules, in this pair of species, the septum is swollen, each side protruding into its respective locule (fig. 38). Consequently, the locule appears as a narrow crescent. In the lower part of the ovary, the dorsal traces, together with numerous lateral traces, separate from the peripheral ring of bundles. Since these unite in varying degrees at the top of the ovary, it is difficult to decide how much of the dorsal strand in the style consists of the distal portions of one or more lateral traces. The calyx consists of a mere rim or short tube, which is scarcely perceptible macroscopically. Moreover, the rim or tube is devoid of vascular tissue; for though in all the flowers examined some of the stamen bundles divide, all of the centrifugal traces so formed terminate in the ovary wall (fig. 29). In only one flower do all four stamen bundles divide; two flowers have three dividing. A flower with two and one with a single stamen bundle branching were also found. The non-dividing stamen bundles are as large as the dividing ones before the latter fork. None of the petal traces divides.

6. *C. ALTERNIFOLIA* L.f. *A. J. Eames 2957* (C).

Since this species differs anatomically from the preceding one only in having certain characters more reduced, it will suffice to list these:

1. The ventral traces are fused and break up into fewer traces at the region of ovule attachment.
2. The ovular bundle remains unbranched in the ovule.
3. There are fewer lateral traces.
4. The dorsal traces separate from the peripheral bundles in the upper part of the ovary.
5. The stamen bundles do not divide (fig. 30). Though this is generally true, a few flowers show one or two stamen bundles dividing. For the most part, therefore, there is neither external nor internal manifestation of the calyx. Nevertheless, as in *C. controversa*, the stamen bundles are manifestly stouter than the petal traces.

7. *C. OBLONGA* Wall. *A. Henry 11,161* (NY).

In the single bicarpellate specimen examined, the petal bundles give rise to the ventral traces. These differ from those of the generalized floral type in ending as mere stubs in the upper part of the ovary. The ovular supply also differs, for the ovular trace descends below the funiculus and then arches upward in entering the ovule. Poor differentiation makes it difficult to discern the association of the dorsal traces. The sepals apparently derive their supply from both stamen and petal bundles.

The other two serials were buds of tricarpellary flowers (fig. 35). In one, two ventral bundles separate above the base of the locule and are fused as

far as the top of the ovary but the third originates double at the base of the ovary; in the other bud, the three ventral bundles are similar; each is composed of the ventral trace of one carpel and the adjacent ventral trace of the carpel beside it, and each arises at the base of the locule. The ovular bundle

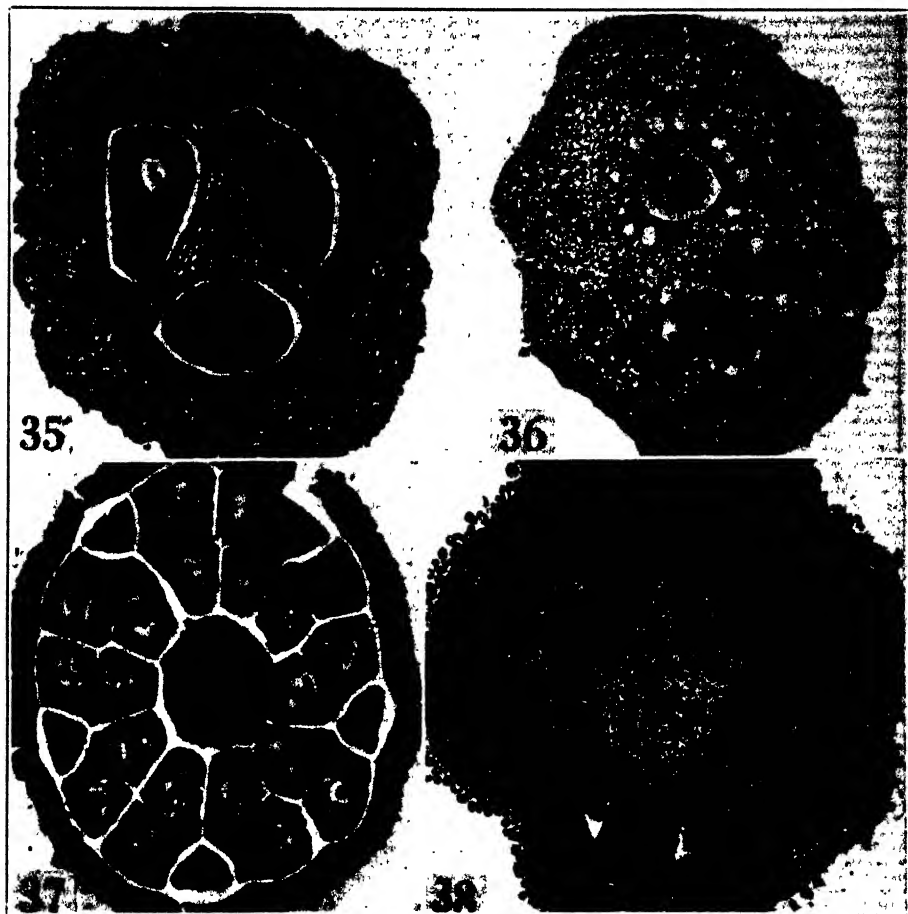


FIG. 35. *C. oblonga*. Cross section of a tri carpellary ovary. FIG. 36. *C. mas*. Large secretory cells surrounding the locules. FIG. 37. *C. Drummondii*. 5-merous flower showing 5 petals and 5 stamens. FIG. 38. *C. controversa*. Septum swollen at region of ovule attachment.

is single. Poor differentiation again makes it almost impossible to determine with which bundles the dorsal and ventral traces are associated. The exact sepal situation is also obscure. Several of the stamen bundles resemble those of *C. mas* in their behavior. The petal trace forms about three strands after entering the petal.

8. *C. DRUMMONDI* Meyer. *C. C. Deam 48559* (C) (as *C. asperifolia*).

The ventral traces of this species, though extremely variable, seem to come principally from the stamen bundles and tend to be separate most of their length. Regularly, however, they enter the style. Though the dorsal trace seems to be associated with the stamen bundle in one flower, in others it is difficult to trace. Among the *Thelycrania* the sepal supply of this species, besides being variable, is the most extensive and complex (fig. 22); the sepal traces derived from the petal bundle often branch and the stamen bundle may divide radially as well as tangentially. The trace cut off tangentially may cleave into three branches as in *C. mas* (fig. 23), or it may give off just a single lateral branch. Various combinations and intergradations of these types of supply are encountered.

One flower of this species is 5-merous (fig. 37). Since it has a bicarpellate ovary, its carpellary supply is not unusual. The number of peripheral bundles in the body of the ovary, however, is ten instead of eight. Anatomically, therefore, it differs little from the general pattern in the genus.

9. *C. BRACHYPODA* Meyer. *C. Y. Chaio 2632* (NY) (as *C. macrophylla*).

In this species, the ventral bundle arises at the base of the ovary and the traces remain fused the greater part of their length. The supply thereafter is that described for the generalized floral type (fig. 13). The dorsal traces separate from the two stamen bundles alternating with those from which the ventral traces arise. The sepal supply of this species resembles that of *C. mas* (fig. 23).

10. *C. GLABRATA* Benth. *A. Kellogg 1866* (C).

The ventral bundles are quite variable in this species. In one flower, both ventral bundles arise at the base of the ovule; in two flowers, one ventral bundle separates in the lower part of the ovary, the other in the upper. All, however, are associated with stamen bundles and remain united to the top of the locule. Except that the ovular traces are only slightly bowed and scarcely arched, the ventral and ovular supply differs little thereafter from that of the generalized type. The absence of lateral traces aids in following the dorsal traces to their origin from the stamen bundles. The sepal supply is rather consistently like that of *C. mas* (fig. 23). All but one stamen bundle divide tangentially; the exceptional stamen bundle has a trace separating radially from each side.

11. *C. RACEMOSA* Lam. *J. H. Kellogg 423* (C) (as *C. paniculata*).

The ventral traces separate at the base of the ovary from the stamen or petal bundles. The arc of ovule traces is not so wide as that of the generalized floral type nor do the ventrals enter the style (fig. 14). In the ovule, the

ovular bundle forks before dividing further. Since there are numerous lateral traces in this species, it is difficult to distinguish the dorsal traces from these. The sepal supply seems to be derived from one like *C. mas*. Instead of dividing tangentially to give a trace which gives rise to a lateral branch on each side, however, one or two stamen bundles in each flower cut off a trace from both ends (fig. 25). The plane of division may be tangential or almost radial.

12. *C. STRICTA* Lam. W. S. *Blatchley* 39 (C).

The ventral bundles of this species are even more variable than those of *C. glabrata*. They may separate in the lower or upper part of the ovary, from the stamen or petal bundles, or both; they may be fused up to the departure of the ovular traces—or one ventral bundle may be double, the other, united; finally, they may end in the ovary or enter the styler column. The dorsal traces also arise either from petal or stamen bundles. There are no lateral traces in the carpels. Though the vascular supply to the sepal is very similar to that of *C. mas*, it differs in that a single bundle is derived tangentially from the stamen bundle (fig. 24a). This bundle then gives off a lateral branch on each side (fig. 24b). These side branches, like those of *C. mas*, unite with the adjacent trace from the nearby petal bundle.

13. *C. ALSOPHILA* W. W. Smith. *J. F. Rock* 17,228, 16,142 (NY).

It is the stamen bundles, in this species, which are united at the base with the ventral traces. The latter are sometimes fused, sometimes separate. Except that the ovular bundle branches sparingly, the behavior of the ventral supply is very similar to that in the generalized flower type (fig. 15). The rest of the carpellary supply consists of dorsals, which are difficult to follow to their origin. The sepal supply is sometimes like that of *C. mas* (fig. 23), sometimes simply three-traced.

14. *C. RUGOSA* Lam. *Flora of Northern U. S.* 376 (C) (as *C. circinata*).

From their origin from the stamen bundles, the ventral traces remain separate and thereafter resemble the ventral traces of the generalized type in their behavior (fig. 13). The dorsal traces are associated either with the stamen or petal bundles, and like the laterals, are weakly differentiated. Unlike the sepal supply in most species described, the derivation of sepal traces from the petal bundles is quite similar to that of the stamen bundles, for usually each stamen and petal bundle gives rise to two sepal traces.

15. *C. AMOMUM* Mill.

The ventral traces of this species resemble those of *C. glabrata* in their variability. Though they regularly arise from the petal bundles, they vary in the extent of union of the two unrelated ventral traces, for fusion of the traces both half the length of the ovary and the full length are encountered.

Moreover, in two flowers both conditions appear in the same ovary. The ovular traces are extremely heavy, and are bowed and arched only slightly as compared with the ovular traces in the generalized floral type. Within the ovule, the ovular bundle forks, then branches distally. For the most part, the intermediate strands of the ventral bundle are not distinct strands, for they join with the ovular traces and with one another. Because the cells of the ovary are abundantly supplied with mucilage, and since the mucilage stains with crystal violet as does the vascular tissue, the origin of the dorsal traces is obscured. However, in part of the serials examined, the dorsal traces seems to be connected with the petal bundles. Difficult to distinguish from the dorsal traces are a few lateral traces. The sepal trace is evidently derived from a three-traced type, i.e., one having a trace from the stamen and each of the two adjacent petal bundles. Yet it is evident from the diversity seen that the sepal supply is not yet stabilized; for though only one or two sepals in each flower are truly three-traced (fig. 26), there are various intergradations between a completely 3-traced sepal and a sepal with a single trace from a stamen bundle. One flower has one sepal 3-traced and the rest simulating a 3-traced supply with a branched trace from the stamen bundle similar to that of *C. mas*.

16. *C. STOLONIFERA* Michx.

In this species, the ventral traces usually separate at the base of the locule from the stamen bundles and continue fused for the greater part of their length. They may, however, separate at the base of the receptacle; they may be derived from petal bundles; and the ventral traces may be united and separate in the same ovary. There are few intermediate ventral strands at the level of the funiculus and the ovular traces are rather light (fig. 16). The ramification of the ovular bundle is the most extensive encountered (fig. 4). Rather peculiarly, the phloem of the ovular trace is on the adaxial surface of the carpel rather than the abaxial side, as might be expected. The dorsal traces diverge from the stamen or petal bundles. There are no lateral traces. Next to *C. alterpifolia*, the sepal supply is most reduced in this species. With the exception of a petal bundle which gives off a single trace radially, the petal bundles do not divide. With respect to the sepal traces from the stamen bundles, only two or three stamen bundles divide (figs. 27, 29, 30). These cut off a single trace which may enter the sepal or terminate in the ovary (figs. 27, 29). One stamen bundle was found which split into three branches. Within the petal, the petal bundle divides into several strands.

DISCUSSION

The marked variation in the floral anatomy of the species described contrasts strikingly with the strong similarity in their gross floral morphology. This variation is seen in the bundles from which the ventral and dorsal

traces separate, in the number of lateral traces present, and in the vascular supply of ovules, petals, and sepals.

Petal Supply. That the vascularization of the petal is undoubtedly secondary is evidenced by two characteristics of such a petal supply. Regardless of how extensively the petal bundle branches, there is always just a single petal trace, which divides only after entering the petal (fig. 6). This vascularization seems to be coincident with the reduction of the calyx and the enclosure of the androecium and gynoecium by the corolla.² This is not to say, however, that the reduction of the calyx caused the ramification of the bundle in the petal.

Most of the other variations, however, are of such a nature that, together with other features of the floral anatomy, they point to a derivation of the genus from a group of plants whose floral structure was quite different from that of *Cornus*. Moreover, there is evidence not only for the structure of the ancestors of this genus, but also for the direction of development in the structure of its descendants: or more simply, there is evidence of evolution progressing as well as past.

Ancestral Flower. There is evidence to believe that the ancestral flower had more members in each whorl than the flower of the present genus. The 5-merous flower found in *C. Drummondii* (fig. 37), and the 3-carpellate ovary in two specimens of *C. oblonga* (fig. 35) and a flower of *C. mas* can be cited. The theory is further supported by the gross floral structure of other genera of the family, for *Mastixia*, *Toricellia*, *Helwingia*, *Corokia*, *Griselinia*, and *Melanophylla* have 5-merous flowers; and 3-carpellate flowers are found in *Toricellia*, *Helwingia*, and sometimes *Melanophylla*. These facts would suggest therefore that the ancestral flower was 5-merous.

Interesting light is cast on this point by the variation in the bundles with which the ventral bundles are united. These may be derived from the stamen bundles, as is always the case in *C. canadensis*, *C. rugosa*, *C. glabrata*, *C. brachypoda*, and *C. suecica*; they may be associated with the stamen bundles in some flowers and the petal bundles in other flowers of the same species, as in *C. alternifolia*, *C. florida*, and *C. stolonifera*, or in the same flower one may separate from the petal bundle, the other from the stamen bundle, as in some specimens of *C. Drummondii*, *C. controversa*, and *C. mas*. The dorsals likewise, both among the various species and among the various flowers of the same species, vary in the bundles with which they are fused. This wide variation is indeed unaccountable in a flower as regular as that of this genus. On the other hand, if one assumes that the flower of *Cornus* has been derived from a 5-merous flower, the extraordinary variation becomes explicable. In

² A similar condition of reduced sepals and highly vascularized petals is found in *Hedera Helix* and species of *Alangium*.

a reduction from five to two carpels, either two adjacent carpels, or a carpel and either alternate carpel would persist. Such a reduction would result in an ontogenetic rearrangement of the carpels. The developing carpels would vary therefore in their orientation with respect to the outer whorls. Coupled with this decrease in the number of carpels would be the reduction of the outer whorls from five to four members. These two changes interacting with each other would make the various combinations described above quite possible; and the ontogenetic nature of these changes might explain the instability within a species and among them.

Vestigial bundles are often the only remnants of structures once present. In *C. alsophila*, *C. brachypoda*, *C. florida*, and occasionally in other species, one or two traces terminate in the receptacle; yet since there is so little uniformity in their position, number, and grouping, it is difficult to discover their essential character. This lack of uniformity may, as above, be due to the reduction in the number of the members of the floral cycles. Nevertheless, whatever their exact nature, they are an indication of other members of the floral whorls now absent.

On the other hand, the abortive carpel found in specimens of *C. florida* and *C. canadensis*, and all the specimens examined of *C. suecica* (fig. 34), suggest that this reduction is proceeding in the present-day members of the genus. Again, this change is to be seen already in other members of the family (*Mastixia*, *Aucuba*, *Griselinia*).

Calyx in the Ancestral Flower. The sepal supply suggests that the calyx also has had an interesting evolution. In the genus today, the calyx is usually small; it consists of four teeth or lobes in most species and of a mere rim in a few. Anatomically, however, in most of the species, especially the three-traced ones, the sepal supply is extraordinarily extensive and heavy for sepals so minute.

C. florida is conspicuous in the extreme vascularization of its calyx. Here both the traces derived from the petal bundles and those from the stamen bundles branch freely, providing many bundles in the calyx (fig. 21). So extensive a supply is approached only by *C. Drummondii* (fig. 22). In *C. mas*, (fig. 23), on the other hand, only the trace cut off by the stamen bundle divides. In this respect, several other species resemble it, viz., *C. brachypoda*, *C. glabrata*, *C. racemosa*, *C. stricta* (fig. 24b), *C. alsophila*, and *C. oblonga*. In *C. Amomum* (fig. 26) there is no ramification of the three traces, and intermediate between this condition and that in *C. mas* is the supply of *C. rugosa*. The reduction has proceeded in *C. canadensis* (fig. 27) and some specimens of *C. suecica* (fig. 27) to an elimination of the two lateral traces, so that the sepal is supplied only by a median trace derived from the stamen bundle. In the two alternate-leaved species and in *C. stolonifera*, some of the stamen bundles even fail to divide (fig. 30). Moreover, in bundles that

do divide, the trace which in other species enters the sepal, here terminates in the ovary (fig. 29).

It is evident, therefore, that in these species of *Cornus* there are sepals with a single trace and sepals with three traces.³ However, this distinction cannot be used to divide the genus, since specimens of *C. stolonifera* and *C. suecica* (fig. 28) occasionally show traces derived from petal bundles. Moreover, such a division would result in a grouping of *C. suecica*, *C. canadensis*, *C. controversa*, *C. alternifolia*, and *C. stolonifera*; an exceedingly unnatural grouping, for it separates *C. stolonifera* from the rest of the *Thelycrania* and places the two alternate-leaved species in the same division as the two suffrutescent species. Nevertheless, the one- and three-traced conditions together with their variations are significant, for they indicate the trend in the reduction of the sepals.

Anatomy suggests that the sepals of the ancestral flowers were foliaceous. Externally they have become very small, and, correspondingly, the vascular supply has become less extensive. But in many species, this internal reduction has not proceeded so far as the external one. In addition, the extreme reductions observed indicate that this reduction will tend toward a disappearance, not only of the sepals themselves, but also of the sepal traces.

Nature of the Septum. Superficially, this genus has a bilocular ovary with axile placentation; actually, observations almost necessitate the conclusion that the ovary was once unilocular with two well-developed parietal placentae.

Most of the species today show no special histological development of the placenta: the placenta is apparently only a locus. In the two alternate-leaved species, however, the swelling of the septum at the region of ovular attachment can only be considered as placental in nature (fig. 38). But this placenta is not a typically axile one.

Even the anatomy is that of parietal rather than axile placentation. In all the species studied, the ventral traces never turn inward in the receptacle, as is the case in axile placentation. Instead, from the receptacle, they proceed directly toward the ovary wall (fig. 1). Moreover, the ventral traces remain in the ovary wall, in no case entering the septum (figs. 3, 4).

In itself, the specimen of *C. suecica* with incomplete septation of the ovary is insufficient evidence for parietal placentation; in view of the above facts, however, the specimen is quite suggestive. Here, the two projections into the locule have the position of parietal placentae (fig. 32). They do not extend to the top of the ovary, a fact which may account for the absence

³ The interpretation of the type of sepal supply found in *C. rugosa* as 3-traced is supported by the fact that the leaves of the members of this family are regularly 3-traced (12), and that 3-traced sepals are found in species less advanced in other characters also. It is worthy of note that the reduction to the single trace has taken place in the sepals before it has occurred in the vegetative member.

of ovules and non-separation of the ventral traces from the outer ring of bundles.

Anatomy also indicates that the placenta was once more extensive than it is today. Significant in this respect is the number of traces derived from the ventral bundle at the region of ovule attachment. In some species, there are many branches, but only a few actually enter the ovules. The other branches are undoubtedly also ovular traces, for they are identical with the traces supplying the ovules, in derivation, position in the ovary, and course—they differ, in fact, only in not entering an ovule (fig. 1). Moreover, occasional flowers of *C. alternifolia*, *C. suecica* (fig. 11d), *C. stricta* (fig. 18), and *C. stolonifera* (fig. 17) show a branching of an ovular trace. This indicates that at one time these were placental bundles which probably branched. Finally, the periclinal arc of ovular traces found at the level of ovule attachment in the ovary wall of some species [*C. controversa*, *C. alternifolia*, *C. brachypoda* (fig. 13), *C. racemosa* (fig. 14), *C. rugosa* (fig. 13), *C. glabrata*, *C. stricta*, *C. Drummondii*] indicates that the placenta might have covered more of the ovary wall than it does at present. Besides extending periclinally, the placentae must also have reached well into the locule for fusion to have occurred.

The septum, therefore, is placenta rather than ovary wall: It has resulted from fusion of two parietal placentae rather than fusion of parts of the walls of the two carpels.

Ovule—Evolutionary Changes. From the vestigial ovular traces, it is clear that the uniovulate carpel of *Cornus* is descended from a multiovulate carpel. Anatomy indicates, in most species, that it is an outer ovule which persists. First, in the species studied, the vestigial ovular traces, when present, are included between the functional ovular traces (figs. 13, 14). Secondly, some species show a bowing of the ovular traces (fig. 13). This bowing may mean that the ovule has moved toward the center, since ordinarily, an ovule so situated with respect to the ventral trace would have a trace running directly to it.

The reduction in the number of ovules has complicated the supply of the surviving ovules, for unlike most ovules, the ovule of *Cornus* receives a bilateral supply, i.e., it receives a trace from each of the two ventral traces of the carpel. In some species, these two bundles are distinct within the ovule. This double supply can only mean that, recently in the phylogeny of the group, each carpel had two ovules, one on each margin. When one of the ovules no longer develops, its persistent ovular trace enters the remaining ovule. In several species some of the intermediate traces fuse with the outer traces, which supply the ovules. In these species, the ovule receives the supply of not two, but several ovules. The extraordinarily heavy bundles in many of the species [*C. florida* (fig. 8), *C. canadensis* (fig. 10), *C. alsophila*, *C.*

glabrata, *C. Drummondi*, *C. racemosa* (fig. 14), *C. stricta*] represent without doubt advanced stages of fusion of the intermediate and outer ovular bundles.

There is also evidence for the direction in which the ovary may evolve. The occasional flowers with an abortive ovule (*C. canadensis*, *C. Drummondi*, *C. suecica* (fig. 34)) forecast a uniovulate ovary. Accompanying this reduction in gross structure will probably be a reduction in the vascular supply. *C. suecica* can be cited as evidence for this, for here are found fusion of the ovular traces derived from the same ventral bundle (figs. 11a-11e) and occasionally elimination of the double supply to the ovule (fig. 11d).

Conclusions of Other Students of the Family. As stated in the introduction, the little that has been published in the floral anatomy of the *Cornaceae* has come from Horne, Martel, and Baillon. Of these, Horne and Martel have dealt with *Cornus*.

Horne (8) has made a comparative study of ten genera of the *Cornaceae*. Several of his observations and conclusions are of interest in connection with the observations and conclusions recorded above. He considers the possibility that the style may be composed of the styles of four carpels and gives Clarke's interpretation of the 4-lobed stylar canal. Clarke (4) concluded from his observations that the styles of two carpels made up the style. In the 4-lobed stylar canal, he interpreted two of the canal lobes as "marginal" and two "sutural." Moreover, Clarke found that in a trilocular ovary there were two additional lobes in the stylar canal for each extra locule, one "marginal," one "sutural."

In the present study, though no special study of the style was made, the shape of the stylar canal was recorded for each specimen. In many species, the stylar canal varies in shape from base to apex. Just above the locules, the canal in transverse section is more or less linear, gradually becoming S-shaped, Y-shaped, and H-shaped in turn, and at the very apex, 4-lobed (fig. 20). In *C. alsophila*, *C. Amomum*, *C. Drummondi*, *C. controversa*, *C. glabrata*, *C. brachypoda*, and *C. stricta*, the canal is eventually H-shaped or 4-lobed. However, in *C. alternifolia*, *C. canadensis*, *C. florida*, *C. mas*, and *C. succica*, the stylar canal remains more or less linear throughout the style. Contrary to Clarke's observations, all the 3-loculate ovaries found have 3-lobed stylar canals (fig. 19). An explanation therefore is required which will account for 3-lobed stylar canals in tricarpeillary ovaries of this genus, and 4- or 2-lobed (linear) stylar canals in bicarpeillary ovaries. Clarke's interpretation does not adequately explain these observations. Rather than that two stylar canal lobes are associated with a style, it seems more likely that one canal lobe corresponds to each style. Where three carpels are present, there is a 3-lobed stylar canal; where two carpels, a 2-lobed (linear) stylar canal. Where four or more stylar canal lobes are found, the situation is more complicated. It is quite evident that the flower of *Cornus* has been

derived from a polymeric flower, which in many cases has been a completely tetrameric one. Vestiges of the polycarpellary or 4-carpellary condition may therefore be expected. Now, it is common for cohesion to occur acropetally, so that a compound pistil may have several separate styles; a corolla tube, several lobes distally. May not reduction, therefore, proceed in the same direction? The basal part of a carpel may be submerged and disappear before the styles. This would explain the presence of a 4-lobed stylar canal in a bicarpellary pistil: two of the styles are sole remnants of their respective carpels. More light might be thrown on this problem by a special study of the vascular supply of the style in the various species. The problem is complicated, however, by the presence of ventral traces in the base of the style and the secondary ramification of the dorsals in the upper part of the style.

With respect to the other genera that Horne studied, several interesting correlations present themselves in placentation and ovular supply. Evidence for parietal placentation can be found. First, in *Aucuba*, when an ovary is biovulate the two ovules are attached on opposite sides of the ovary wall, so that the placentation is parietal. Also, a situation parallel to the abnormal ovary of *C. suecica* is found in some specimens of *Marlea*. In this genus Bentham and Hooker (2) state that the ovary may be unilocular in the upper and trilocular in the lower portion. Clarke also noted this condition, in *M. begonifolia*. Finally, Horne lists as a difference between *Cornus* and *Corokia* the fact that the latter genus has parietal placentae immediately above the ovule. In view of the discussion above, this would be considered a similarity! On the other hand, two pieces of evidence may be cited in favor of axile placentation. First there is the very definite axile placentation in *Helwingia*. Neither Horne nor Descaisne (5), however, believes that this genus belongs in the *Cornaceae*. A more cogent objection is the central strand in the septum of *Corokia*. Since the origin of this strand is not given in Horne's paper, however, material must be examined before an explanation is ventured.

The compound ovular supply of *Cornus* is seen in *Corokia*, *Griselinia*, *Nyssa* also, and to a limited extent in *Aucuba*. Horne also recognizes that (in *Corokia*) there may be a "diversion of the vascular tissue pertaining to the absent ovules to the present ovule."

Whereas Horne has studied a majority of the genera of the *Cornaceae* Martel (11) has studied a single species of *Cornus*, upon which he bases his comparison of the family with the *Araliaceae* and the *Umbelliflorae*. Moreover, Martel emphasizes histological structure and is thereby led to erroneous or superficial statements. For example, he states that except for the vascular supply, the calyx, with respect to the parenchyma of which it is made up, can be considered simply a prolongation of the receptacle. (As will be seen, Martel believes the ovary is enveloped by the receptacle.)

He considers that the 4-lobed stylar canal indicates that there are four carpels, but states that they are reduced at the base by atrophy or fusion following upon a limitation in the space allowed them to develop. He does not make clear whether he believes this atrophy or fusion to be ontogenetic, or phylogenetic.

He concludes that the placentation is parietal, because the "placental" bundles remain in the ovary wall. Like Horne, he does not recognize these "placental" bundles ("peripheral" bundles of Horne) as the ventral bundles. In fact, he even states that the "commissural" (ventral) bundle is absent.

With respect to the bilateral ovular supply, he states that it is notable that the "funiculi" (ovular traces) derived from both placentae of the carpel enter the same ovule, just as if the placentation were axile. It is assumed that he means that type of axile placentation in which the two ventral traces of a carpel have fused. Yet what evidence is there to believe that in such cases the ovular supply is bilateral, i.e., composed of an ovular trace from each of the two ventral traces of the carpel? In fact, there is evidence to the contrary. First, in axile placentation, the ventral traces of adjacent carpels unite more commonly than do the ventral traces of the same carpel. **Moreover**, even when the ventral traces of the same carpel are separate, it is very unusual for an ovule to receive a trace from each ventral trace. There is little basis, therefore, to conclude that after the ventral traces have united, the ovular trace is double. Martel's parallelism is, therefore, merely an analogy and can have little significance in establishing the type of placentation found in *Cornus*.

Martel interprets the separation of the outer ring of bundles from the carpellary bundles as a more marked separation of receptacle and ovary in *Cornus* than is found in the *Umbelliflorae*, *Hedera*, and *Aralia*. Had Martel examined other species of *Cornus* and observed how often the dorsal traces are united with the peripheral bundles the length of the ovule, he would have avoided such a generalization. He states, furthermore, that from the inferior ovary of *Cornus* to a superior ovary it is only a short step, which consists simply of a more profound differentiation of perianth and androecium. Such a differentiation could only be from the outer portion which he considers receptacular. Stamens, petals and sepals so formed would be appendicular in nature in the upper portion and axial in the lower portion. These would indeed be anomalous floral members.

Taxonomy. A comparative study of the floral anatomy of a group should reveal the extent of specialization of the various members so far as their flowers are concerned, thus aiding in establishing the relationship among them. It must be remembered, however, that all the characters of a species do not evolve at the same rate; in fact, some may, for a time, remain

unchanged or even retrogress. Moreover, changes vary in their significance, both in themselves, and in comparisons among different species. For instance, in the species of *Cornus*, the supply of the petal is of little phylogenetic importance, as compared with the variation in the supply of the ovule. On the other hand, though the extent of fusion of the ventral traces is in itself significant in indicating evolutionary advancement, it can scarcely be used in this genus, since the character often varies within the species itself. The situation in the sepal supply is quite the reverse, for here the degree of change, important in itself, is consistent within the species. In evaluating the relative progress of the various species, therefore, the sum total of the various advanced traits together with their significance must be considered.

Among the species studied, *C. florida* is anatomically by far the least specialized. It has the most extensive sepal supply (fig. 21); the ovule supply is very heavy (fig. 8); and without exception there is a "vestigial" trace in the receptacle. In other species such traces occur only occasionally, if at all. At the other extreme are the anatomically highly specialized *C. alternifolia* (fig. 30), *C. stolonifera* (fig. 30), and *C. suecica* (fig. 30). In all three, the vascular supply to the calyx is absent or incomplete. *C. alternifolia*, with no sepal traces and the calyx reduced to a mere rim, shows the most extreme reduction externally as well as internally. In ovule supply, all three have relatively light ovular traces, but *C. suecica* shows the most specialized condition (figs. 11a-11e). Moreover, *C. suecica* regularly shows the abortion of one ovule and often a decrease in size of the corresponding carpel (fig. 34). Of the three, therefore, this is probably the most highly specialized. ●

In Wangerin's treatment (13), the species studied fall into the following sub-groups:

Subgenus *Benthamidia*

C. florida

Subgenus *Macrocarpium*

C. mas

Subgenus *Arctocranius*

C. canadensis

C. suecica

Subgenus *Thelycrania*

Section *Bothrocaryum*

C. controversa

C. alternifolia

Section *Amblycaryum*

Subsection *Albidae*

C. racemosa

C. stolonifera

C. Drummondii

C. rugosa

C. glabrata

C. stricta

Subsection *Oblongifoliae*

C. oblonga

Subsection *Nigrae*

C. alsophila

C. brachypoda

Subsection *Corynostylae*

C. Amomum

The floral anatomy does not strongly support the taxonomic groupings within the genus. The following comparison is based primarily on the sepal supply, since the stages in its evolution are rather completely represented in the species studied. *C. florida* is anatomically sufficiently distinct to be segregated from the other species and in this respect sufficiently unspecialized to represent a type ancestral to them. From this species, *C. mas* may represent a step in the reduction. In this involucrate series, extreme reduction is reached in *C. canadensis* and *C. suecica*. These two suffrutescent species are macroscopically strikingly similar. Microscopically also, in their sepal and petal supply, and in the frequent abortion of one ovule, they are similar. Yet the ovule supply of *C. canadensis* (fig. 10) is so heavy and "primitive" in comparison to the extremely fused supply of *C. suecica* (figs. 11a-11e), that, phylogenetically, the two species must be quite distant. Either they have developed along divergent lines from a "common ancestor," or more likely *C. suecica* has evolved so much more rapidly than *C. canadensis*, that there is now a wide breach between them.

In the non-involucrate species (subgenus *Thelycrania*), the opposite-leaved species are placed in the section *Amblycaryum* apart from the alternate-leaved species. Most of the opposite-leaved species have a sepal supply so similar to that of *C. mas* (fig. 23) or so evidently a modification of such a supply, that it seems quite possible that they have had a common origin close to that of *C. mas*, and a development rather parallel. Anatomically, the members of the section do not segregate into groups. *C. oblonga* has been inadequately studied, but the double arching of the ovular trace makes it unique. Among the rest, *C. Drummondii* (fig. 32) has a sepal supply which, in its extensive ramification, approaches the supply of *C. florida* (fig. 21). The other species more closely resemble *C. mas* (fig. 23). Very similar to the sepal supply of *C. mas* is that of *C. brachypoda*, *C. glabrata*, *C. racemosa*, *C. stricta*. The supply of *C. brachypoda* is most regularly like that of *C. mas*, whereas occasional stamen bundles of the other species diverge from this. Progressive reduction is seen in *C. alsophila*, *C. rugosa*, *C. Amomum*, and *C. stolonifera*, flowers of the last species showing some sepal traces absent (fig. 30). In a general way the ovular supply supports the two groupings but there is not enough variation in this character among the species to indicate relative progress among them. The above does not imply that the two groups are considered "natural" or that the members of the section can be arranged in ascending order with *C. Drummondii* at the foot. Rather, these species seem to form a plexus, some of them more advanced than others, but most of them so closely related, phylogenetically, as to make it difficult to select the main lines of development.

The alternate-leaved species are sharply set apart from opposite-leaved species. The internal structure supports this separation, for *C. controversa*

and *C. alternifolia* are characterized by the presence of a prominent placenta (fig. 38), extreme arching of the ovular traces, and short (or absent) sepal traces (figs. 29, 30), which never enter the minute calyx tube or rim. In addition to the above characters, the two species resemble each other in having numerous lateral traces in the carpel. Of the two, *C. alternifolia* is more advanced since it rarely has sepal traces; the calyx is a mere ridge; and the ovular supply is not extensive. The anatomy of the two species is so specialized, however, that it is difficult to be certain anatomically, that the pair are distal twigs on a side shoot of the *Thelycrania* limb of the phylogenetic tree of *Cornus*.

SUMMARY

A detailed study was made of the floral anatomy of sixteen species of the genus *Cornus*.

The evidence obtained suggests the following conclusions:

1. The ancestral flower had more members in each whorl than the flower of the present genus.
2. The sepals in the ancestral flower were foliaceous, in contrast to the minute sepals characteristic of the genus today.
3. The bilocular ovary with reduced placenta is derived from a unilocular ovary with two well-developed parietal placentae.
4. Morphologically, the septum represents two placentae fused.
5. The uniovulate carpel is derived from a multiovulate carpel.
6. The vascularization of the petal is undoubtedly secondary.

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STRUCTURE AND DEVELOPMENT OF SCLEREIDS IN THE PETIOLE OF *CAMELLIA JAPONICA* L.

ADRIANCE S. FOSTER*

INTRODUCTION

This paper describes the results of a study of the structure and development of the remarkable thick-walled and grotesquely branched cells which occur in the parenchyma of the leaf of *Camellia japonica*. These elements were discovered and illustrated nearly a century ago by Mirbel and Payen (1849, 1850) and have proved to represent one of the definitive histological characters of the majority of genera in the Theaceae (Kochs 1900; Solereder 1908; Beauvisage 1920; Melchior 1925). Despite the frequent reference to these cells in general texts and in the scattered literature on "sclerenchyma," little is known about the details of their developmental history. Indeed, aside from the brief account given by Buch (1870), the investigations of Cavara (1897) appear to be the only effort to explore the origin and growth of these cells. Cavara, adopting a term originated by Sachs (1882), designated the isolated branched cells in *Camellia* as "idioblasts." He stated that the ramified character of the cell results from a true intercellular growth of the wall between neighboring tissue-elements during early phases of ontogeny. If Cavara's conclusion is correct, the idioblasts of *Camellia* should offer interesting material for a study of the much-disputed phenomena of "gliding" or "intrusive" growth (Majumdar 1941; Sinnott and Bloch 1939, 1943).

But in addition to their morphogenetic interest, the branched cells in the leaf of *Camellia* pose a further question, viz.: what is the morphological nature of such extraordinary cells? Reference to table 1 will show that eleven distinct histological terms have been applied to these elements. A discussion of this exceptionally confusing nomenclature must be postponed until the observational data in this paper have been presented. Here it is only essential to emphasize that this confusion in terminology is by no means restricted to *Camellia*. Cells which appear fundamentally similar at least in form to those in *Camellia* occur in a large number of angiosperm groups as well as in certain gymnosperms (Thomas 1865; Seward 1906; Solereder 1908). The nomenclature for these elements includes many of the terms listed in table 1. It is thus evident that the entire problem of so-called "sclerenchyma" merits careful re-examination. It is hoped that the present study may serve to stimulate and to orient intensive as well as extensive investigations in both angiosperms and gymnosperms.

* Plates 2 and 3 are published with the help of a contribution by the author and of the Lucien M. Underwood Memorial Fund.

For convenience and brevity, Tschirch's (1885) term "sclereid" will be employed in the descriptive sections of this paper. A brief account of the origin and applicability of this term to sclerenchymatous elements has already been given in a recent book by the writer (Foster 1942, p. 67-70).

MATERIAL AND TECHNIQUE

The leaves of *Camellia japonica* used for this investigation were collected from vigorous plants growing on the campus of the University of California at Berkeley. The horticultural variety represented by these plants could not be determined, however, because of the variable character of the flowers. For comparative purposes, a brief study was also made of the sclereids in the leaves of *Camellia reticulata* Lindl. and *Camellia sinensis* (L.) O. Ktze. Material of the later species was obtained from plants in Golden Gate Park, San Francisco, through the kindness of Mr. Eric Walther.

Preliminary study of hand-sections of the leaf of *C. japonica* showed that the sclereids are most abundant in the petiole. Consequently this portion of the leaf served as the basis for all developmental studies. Young as well as mature petioles were cut transversely into sectors and fixed for 24 hours in a mixture of formalin-acetic acid-ethyl alcohol according to a formula given by Sass (1940, p. 16). Dehydration, clearing with xylene, and infiltration with paraffin were carried out using the general procedure recommended by Ball (1941). Serial trans- and longisections 6-8 μ in thickness were easily secured from young petioles in which the sclereids are thin-walled. But for maturing and adult sclereids, it was necessary to soften the material. To accomplish this, a small portion of the tissue of the imbedded petiole was exposed by trimming away the paraffin and the block then immersed for 2-3 days in a solution of glycerine-alcohol (90 cc. 60 per cent alcohol; 10 cc. glycerine). By this method, thin and usually unscratched serial sections could be obtained with little difficulty. A modification of the tannic acid-iron chloride-safranin method was adopted for staining the sections (Foster 1934). This involved the use of a 0.5 per cent aqueous solution of tannic acid in which the slides were placed for five minutes before transfer to the iron chloride. The preparations were then washed thoroughly in running water and counterstained for 24 hours or less in safranin. This slight modification of the writer's previous method resulted in a sharp and pleasing color contrast between the walls of the parenchymatous tissues and the sclereids.

Macerated petioles were found indispensable for a study of the elaborate forms of the adult sclereids. The method of maceration outlined by Priestley and Scott (1938, p. 193-194) gave excellent results. Thick transverse sections of fresh petioles were first thoroughly aspirated in acid-alcohol (3 parts

70 per cent ethyl alcohol: 1 part concentrated HCl). New acid-alcohol was then added and allowed to act for 24 hours. After thorough washing in water the material was placed in a 0.5 per cent aqueous solution of ammonium oxalate. Within several days, the parenchyma tissues were sufficiently macerated to permit a ready examination of the isolated sclereids. Permanent glycerine-jelly mounts were made of both unstained as well as safranin-stained material.

Thanks are due the writer's wife, Helen Vincent Foster, for her skillful execution of the perspective drawings of the sclereids illustrated in figures 2-8. Acknowledgment is also made to Dr. Roger Reeve for his generous assistance in imbedding some of the materials used in this study.

DISTRIBUTION OF SCLEREIDS IN THE PETIOLE

When serial transverse sections of mature petioles are examined, it is evident that the sclereids do not form a continuous tissue but are scattered as typical idioblasts¹ in certain definable regions of the "fundamental tissue system" (fig. 1). Sclereids are most abundant in the outer cortical region where they collectively form a discontinuous cylinder of thick-walled polymorphic cells. The tissue in which they lie consists of relatively small cells with inconspicuous air-spaces. In transection these cells very closely resemble collenchyma because of the irregular thickenings of their walls (figs. 23-26). But in longisection the cells are short and cannot therefore be classified as "typical" angular collenchyma. The remainder of the fundamental tissue system is composed of larger thinner-walled parenchyma. Intercellular spaces are particularly well developed in the adaxial portion of this tissue which closely resembles in structure typical spongy parenchyma. While sclereids are found sporadically in the parenchyma near the phloem of the single collateral bundle, they appear more consistently in the midst of the large-celled parenchyma adjacent to the xylem (fig. 1, *ms*). In this pith-like portion, many of the sclereids are particularly large and thick-walled.

As is clearly indicated in figure 1, the greatest dimension of the "cortical" sclereids tends to lie parallel to the epidermis or to the contour of the vascular bundle. This is most clearly shown by the sclereids in the adaxial cortex which lie virtually at right angles to the longitudinal files of cells in which they are imbedded (fig. 26). The significance of this arrangement, which is markedly different from the vertical orientation of "typical" fibers, will appear when the ontogeny of the sclereids is described.

FORM OF THE MATURE SCLEREIDS

A thorough study of both serial sections as well as macerations reveals the remarkable polymorphism typical of the sclereids of *Camellia japonica*.

¹ Occasionally, isolated groups of 2-3 connected sclereids may be seen in following serial sections, but such "nests" scarcely represent a "tissue" (cf. fig. 20).

Cavara (1897) attempted to show that the form of the sclereid is to some extent correlated with its position in the leaf. According to his descriptions, profusely branched forms occur in the parenchyma surrounding the vascular bundle in the petiole and midrib while in the lamina Y-, L-, and T-shaped forms prevail. In the writer's experience, such a distinction cannot be drawn and virtually all of the "form-types" recognized by Cavara may occur in the parenchymatous tissue of a single petiole.

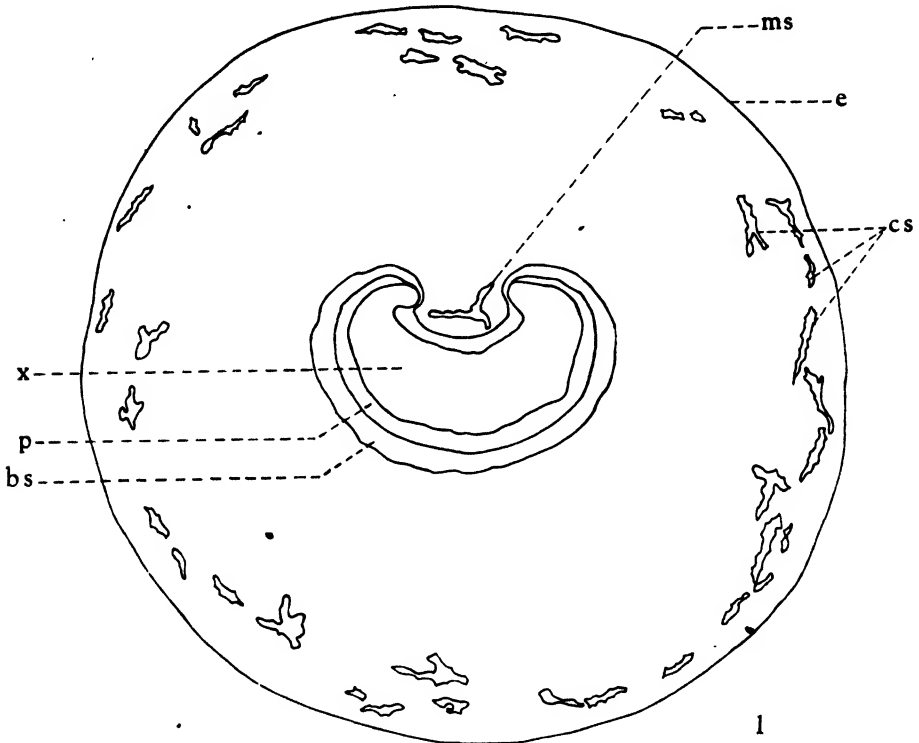


FIG. 1. Transection of the petiole of *Camellia japonica* showing the distribution of the sclereids as idioblasts in the "fundamental tissue system." This illustration was prepared by first tracing in ink the outlines of the epidermis, sclereids and vascular tissues on a photomicrograph which was then placed in a solution to remove the photographic image. Legend: *bs*, bundle sheath; *cs*, sclereids of outer cortex; *e*, epidermis; *ms*, medullary sclereid; *p*, phloem; *x*, xylem. $\times 45$.

Because of the bewildering intergradations in form, it is only possible to point out some of the most commonly recurring form-types. Many sclereids are fusiform and, except for their peculiar oblique or transverse orientation with reference to the long axis of the petiole, resemble in their general form short fibers (figs. 5, 26). Very commonly however the sclereid is branched, often in a most curious fashion. In the simpler type of branching, the cell is roughly Y-shaped with either symmetrical or asymmetrical

arms (figs. 7, 8). In a not infrequent type, the cell is extended in length and provided at one or both ends with a pair of short divergent branches (fig. 6). The most bizarre configuration however is presented by the varied "stellate" types (figs. 2, 3, 19, 23, 24, 25). Such cells consist of a thick central portion from which four or more arms radiate. When the branches are relatively equal and lie nearly in the same plane, the cell might appropriately be designated as an "astrosclereid," following the nomenclature proposed by Tschirch (1885, 1889). But very often cells of this general type are extremely grotesque in appearance, because certain of the arms extend vertically as well as obliquely from the central region (fig. 3). As far as the writer could determine there appears to be no correlation between the form of a given sclereid and its specific position in the petiole. Although branched forms seem to predominate in the "medullary" region (fig. 19), both fusiform and elaborately ramified types occur indiscriminately in the outer "cortex" (figs. 23-26).

Because of the irregular form of the sclereids, accurate measurements of the dimensions of these cells are often impossible to obtain. A series of random measurements of a number of fusiform types indicates that the length may range from 250 to 530 microns while the maximum diameter varies from 20 to 35 microns. These data show that the ratio of diameter to length of the sclereids is considerably less than in many "typical" fibers (cf. Foster 1942, p. 74-75).

The examination of hundreds of cells isolated by maceration reveals one of the most striking and consistent peculiarities of the sclereids of *Camellia*, viz.: the presence of numerous, short, conical or irregular protuberances distributed irregularly on both the main "body" of the cell as well as on its branches. For convenience in description, these processes will be designated as "spicules." As is clearly illustrated by figures 2-8, the relative size and abundance of the spicules are highly variable. Certain of the small sclereids, which occur sporadically in the outer cortex of the petiole, are relatively smooth-walled (figs. 4, 8). But the spicules are often so numerous and closely-spaced on the larger sclereids that such cells have a distinctly "spiny" appearance (figs. 2, 3, 5, 6, 7). Despite the many allusions to the sclereids of *Camellia* in botanical literature, it is a noteworthy fact that the only reference to the distinctive spicules is made by Cavara (1897), probably because he made a careful study of elements isolated by maceration. Neither Kochs (1900), Solereder (1908), Beauvisage (1920), nor

Explanation of plate 2, figs. 2-5

FIGS. 2-5. Camera lucida drawings of adult sclereids isolated by maceration. FIGS. 2, 3. Stellate types. FIG. 4. Weakly-branched type. FIG. 5. Fusiform type. Note the characteristic spicules and the narrow lumina in figures 2, 3, and 5; only a few of the numerous pit-canals are shown. In figure 4, the lumen is broader and few spicules are present. All figures $\times 236$.



2



4



3



5



FOSTER: SCLEREIDS IN CAMELLIA

Melchior (1925) in their anatomical treatments of the tea family refer to the spiculate character of the sclereids. Indeed Melchior (p. 111, fig. 59) simply repeats the familiar figure copied from Tschirch (1889, p. 304, fig. 348) which depicts branched sclereids of *Thea* in sectional as well as isolated view with "smooth" walls. For comparative purposes, the writer made a study of the adult sclereids in the petioles of leaves of *C. reticulata* and *C. sinensis*. In both of these species, the isolated sclereids closely resemble those of *C. japonica* in their form and noticeably spiculate character.

As will be shown later, the spiculate character of the sclereid is acquired during the early ontogeny of the cell as a result of local and restricted extensions of the primary wall. Thin transverse sections of nearly mature sclereids clearly show that the majority of the spicules are truly intercellular, extending for short distances into the middle lamella between adjacent parenchyma cells (fig. 26). Because of such numerous projections, which subsequently develop secondary walls, the sclereid evidently is firmly "anchored" to the tissue-elements which surround it. Spicules also may extend freely into air-spaces which lie near the extensible primary wall of the sclereid (figs. 19, 21, 22, 29). These spicules are readily seen, even in comparatively thick hand-sections of the petiole and it is therefore difficult to see how they were overlooked by such early workers as Buch (1870).

ORIGIN AND DEVELOPMENT OF SCLEREIDS

Despite the varied form-types exhibited by the adult petiolar sclereids, these cells originate from parenchymatous elements of the "fundamental tissue system." This fact is essential to a clear understanding of the remarkable ontogeny of the sclereid. In agreement with Cavara's (1897) observations, the sclereid initials are not morphologically recognizable until the foliage leaf has emerged from the bud and is beginning its final phase of expansion and maturation. In the variety of *Camellia japonica* used in this study, sclereid initials are first evident in leaves 5-6 centimeters long. At this stage, the petiole has reached nearly its full length although it is slightly smaller in diameter than that of the adult leaf.

What criteria distinguish a sclereid initial from neighboring parenchymatous elements? In view of the idioblastic distribution of the initials in both large- and small-celled tissue, it is obvious that neither relative size nor position is a definitive character. According to Cavara (1897, p. 79), the large size of the nucleus clearly demarcates a young idioblast from

Explanation of plate 3, figs. 6-8

FIGS. 6-8. Camera lucida drawings of sclereids isolated by maceration. FIG. 6. Elongated type with dichotomous tips. FIGS. 7, 8. Y-shaped types. Note the abundant spicules and the very narrow lumina of the cells in figures 6, 7. In figure 8, the lumen is broad and the surface of the cell nearly smooth. All figures $\times 236$.

neighboring cells. This conclusion is supported by the present study, and reference to figures 9, 10, and 12 will show the striking size difference between the nuclei of young sclereids and their neighboring tissue-elements. Cavara found that the nuclei of young idioblasts are "14-16 microns in length and 10-14 microns in width while the nuclei of surrounding cells measure only 6-8 microns by 4-6 microns." He further stated that the nucleus of the young idioblast is also distinguished by a prominent central "globular body." The latter is highly-refractive in living nuclei and in his view is not the nucleolus because it is vividly colored by "achromatic stains." The writer's observations on fixed as well as living material confirm the existence of a prominent, more or less centralized body in the nucleus of actively growing sclereid-initials (figs. 9-14). But in many instances the nucleus may exhibit as many as three distinct "central bodies," which superficially at least appear to be nucleoli. No final decision, however, is possible until a thorough study of metabolic and dividing nuclei in the various leaf tissues of *Camellia* has been undertaken.

By utilizing the distinguishing character of nuclear size it is possible to study the walls of sclereid initials prior to the enlargement of these cells. With the techniques used in this investigation, the walls of the initials appear essentially similar to those of the surrounding parenchyma cells. This is particularly evident in the outer cortex of the petiole where the thickened areas of the walls of both cell types exhibit typical primary pit-fields (figs. 9-12). It is therefore clear that the irregular growth of the sclereid as an idioblast must depend first of all upon the ability of its wall to distend at certain points. Careful examination of hundreds of cells shows that the distensible regions invariably occur at the corners where the initial is in contact with the middle lamella separating two adjacent parenchyma cells.

Figures 9-12 illustrate very early stages in the growth of sclereid initials in the cortex of the petiole. In each it is clear that the initial has produced one or more slender delicate, tubular branches which extend between the walls of neighboring tissue elements. As mentioned earlier in this paper, the outer cortical cells exhibit collenchymatous thickenings when viewed in transection. Hence, as is shown in figures 9 and 11, the early tubular extensions of the sclereid must literally force their way through such thickened areas. Whether this is accomplished by the secretion of specific pectin-digesting enzymes, as appears to be the case for many pollen tubes (Paton 1921), remains to be proved. At any event it seems true that the ramification of the sclereid represents true intercellular development. No evidence has been found of either crushed primary walls in invaded parenchyma tissue nor of the penetration of parenchyma cells by the arms of the sclereid.



In some instances, the initial at first produces a single tube-like process which may often be seen in "broad view" directly in contact with one of the primary walls of an adjacent parenchyma cell (fig. 10). Initials observed in this plane of section suggest that the growing tubular-arm does not "avoid" the primary pit-fields between two parenchyma cells. Indeed, it is difficult to imagine how the pit-fields with their plasmodesmata can fail to be split apart at certain regions of the wall. Very commonly, tubular branches arise at two adjacent corners of a sclereid initial. This results in a dichotomous branch between the two arms of which lies a parenchyma cell (figs. 9, 11, 12). The continued development of a dichotomous branch leads to the Y-type of adult sclereid while the formation of additional dichotomies from other corners of the initial results in stellate or irregularly branched types (figs. 2, 3, 7, 8).

Further development of the sclereid involves the gradual enlargement of the main body of the cell and the continued intercellular growth of its tubular branches. As the latter increase in length, their course often becomes so irregular that they cannot be seen as entire structures either in trans- or longisectional view. Cavares's (1897, pl. XXXI, fig. 8) illustration depicts a young stage and gives no idea of the extraordinary undulation and growth in various planes of the arms of branching sclereids. Occasionally, a developing tube may pursue a fairly regular intercellular course because of the more or less regular arrangement of the parenchyma cells in its path (fig. 14). But more frequently, one or more of the arms of a sclereid grow vertically or obliquely with reference to the main body. This has been observed convincingly in longisection (fig. 13) and is readily deduced from the incomplete transections which are usually obtained of advanced stages in sclereid ontogeny (figs. 16, 17).

The behavior of the intercellular branches of sclereids in lacunate areas of the parenchyma is particularly interesting. In the relatively compact

Explanation of figures 9-15

FIGS. 9-12. Transections of early stages in intercellular growth of sclereid initials. Note the large nucleus with its prominent nucleolus in each young sclereid. FIG. 9. An initial with three short tubular branches. FIG. 10. "Broad view" of a tubular branch in contact with the primary wall of a parenchyma cell; note the pit-fields (light areas) in the latter. FIG. 11. An initial with two short intercellular branches. Note the pit-fields seen in section view in the wall of this initial and the typical collenchymatous thickenings of neighboring parenchyma cells. FIG. 12. An initial showing dichotomous branching at lower side. This is also illustrated in figures 9 and 11. FIGS. 13, 14. Longisections of older stages in intercellular development of sclereid initials. FIG. 13. Initial with long, oblique branch the tip of which (lower left) is dichotomous. Note abundant cytoplasm in this branch and the large solitary nucleus. FIG. 14. Initial with delicate branch extending nearly at right-angles to vertical files of parenchyma cells. Note the development of two spicules from the lower wall of the initial at either side of the prominent nucleus. FIG. 15. Transection of the dichotomous branch of a sclereid initial at its point of entrance into a prominent air-lacuna. Note the tenuous character of the primary wall. All figures $\times 550$.

tissue of the outer cortex; the delicate tips of certain of the sclereid branches have been observed to extend freely into small air-spaces. Better examples, however, are provided by those sclereids which originate and develop in the more loosely-arranged parenchyma of the inner cortex and the pith. In these regions, the growing tips of the branches very frequently enter the large intercellular spaces. A striking illustration is shown in figure 15, which depicts the dichotomous end of a young sclereid just penetrating a very conspicuous air-lacuna. Buch (1870, p. 28), who apparently confined his observations to developing sclereids in the mesophyll of the lamina, states that the branch of a sclereid grows freely into an intercellular space "until it fills it completely." Such a phenomenon has never been observed by the writer in the petiole of *Camellia*.² On the contrary, soon after its entrance into a lacuna, the extension of the tip of the tube ceases. At maturity, such intrusive tips may be seen to occupy only a portion of the intercellular lacuna (fig. 21).

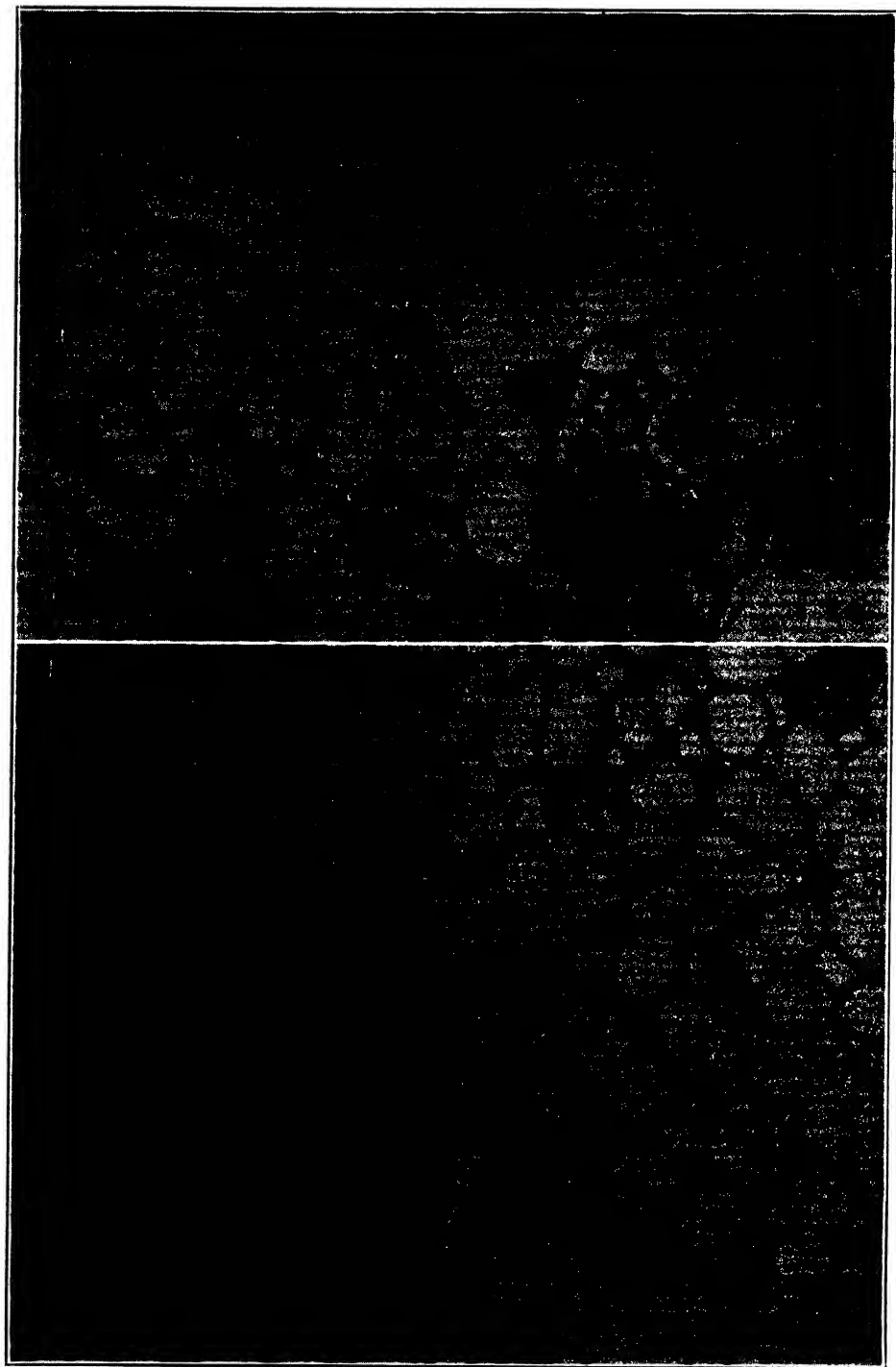
The markedly extensible nature of the primary wall of young sclereids is very clearly illustrated by the development of the characteristic spicules which have been described earlier in this paper. From an ontogenetic standpoint, these structures represent "minor branches" of the cell and only differ in degree of development from the "major branches." Spicules originate during the formation of the major branches and like them are truly intercellular in their growth. As is shown in figures 13 and 14, young spicules appear as short conical protuberances which extend between the walls of certain of the parenchyma cells bordering on the main body of the sclereid and its branches. As is true of the main branches of a sclereid, the tips of the spicules may enter intercellular air spaces (figs. 19, 21, 22, 26). The factors which determine the frequency of intercellular outgrowths and hence the number and distribution of spicules on the mature sclereid are unknown. But it is interesting that the small and presumably less vigorously developing sclereids typically exhibit relatively few spicules (cf. figs. 4, 8). This suggests that wide differences in the physiology of wall growth may exist between sclereids occurring in the same general region of the petiole.

As far as the writer could determine, the protoplast remains uninucleate

² According to Buch (1870, p. 16-18), the remarkable H-shaped sclerenchyma cells in the petiole of *Fagraea auriculata* (Loganiaceae) owe their form to the development of parallel "arms" within the vertical air-spaces bordering the cell. Buch compares these cells and their development with the apparently similar elements found in the aerial roots of *Monstera Lennea* (cf. also the statements by Solereder 1908, p. 539-540).

Explanation of figures 16, 17

Transections of large ramified sclereids at the close of the period of intercellular growth. With the exception of the short pointed spicule at the upper right of figure 16, none of the tips of the branches are in the plane of section. Note the variation in the relative position of the prominent nucleus in each sclereid. $\times 380$.



throughout the entire intercellular growth of the sclereid (figs. 9-14, 16, 17). This contrasts markedly with the multinucleate condition which arises during the extension of certain bast fibers (Esau 1938, 1943). Because of the irregular form which is acquired early by the developing sclereid, interpretations based on serial sections may be open to question. To eliminate this objection, thin slices of petioles were fixed in absolute alcohol-acetic acid, macerated in 50 per cent hydrochloric acid, and smears stained in aceto-carmin. A single large, weakly chromatic nucleus was observed in all immature sclereids which were suitable for study by this technique. During the late phases of secondary-wall formation, the sclereid likewise appears uninucleate (figs. 26, 27, 29-32). According to Puchinger (1923) a single lens-shaped nucleus with two nucleoli is present in the mature sclereids of leaves of *Thea japonica*. Her observations indicate that the sclereids retain their nuclei for as long as three years.

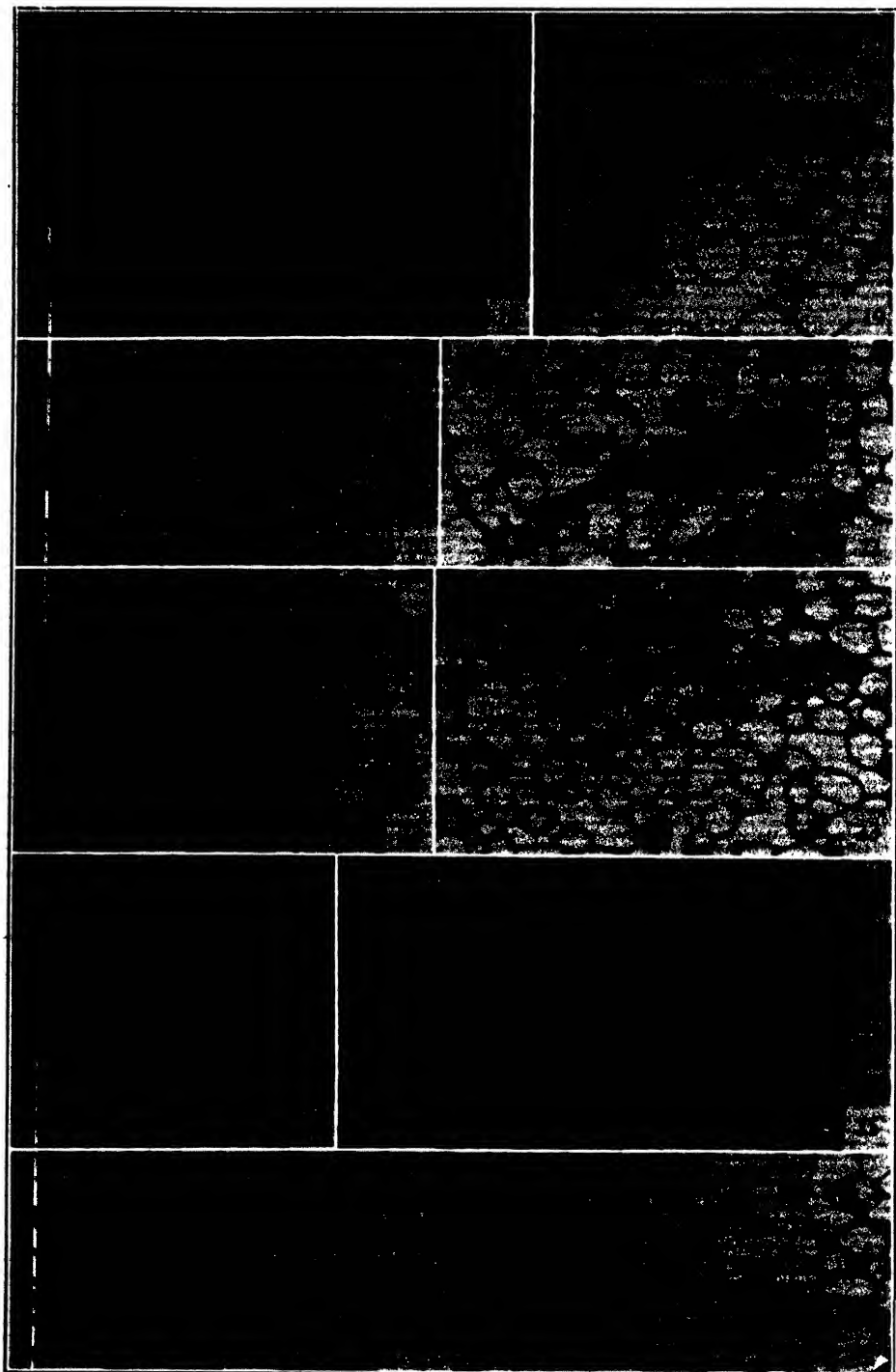
DEVELOPMENT OF THE SECONDARY WALL AND PIT CANALS

During its phase of enlargement and intercellular growth, the sclereid is provided with a thin primary wall. The extremely tenuous nature of this membrane is clearly shown when the intercellular branching of the initial begins as well as in certain favorable sections of older tubes (figs. 9-14). Exceptionally clear views of the primary wall are also obtained at the points of entrance of the delicate ramifications of a sclereid into air-lacunae (fig. 15). When enlargement ceases, the sclereid rapidly acquires a massive secondary wall which may develop to such an extent that the lumen becomes occluded or reduced to a narrow channel, particularly in the branches (figs. 2, 3, 5, 6, 7).

Although the irregular form of the sclereid makes interpretation very difficult, it is probable that secondary wall formation is initiated uniformly

Explanation of figures 18-26

FIG. 18. Transection of ramified sclereid from cortex showing an early stage in the development of the secondary wall. Note the shrunken cytoplasm and the single nucleus. FIGS. 19-22. Transections of sclereids from the pith region of the petiole. FIG. 19. Large branched type with thick secondary wall and abundant ramiform pit-canals. Note the extension of spicules into air-spaces at the lower right and center of this cell. FIG. 20. Two sclereids in contact, the upper represented by a branch shown in transection. A portion of the vascular bundle appears at the right of these sclereids. FIG. 21. Sclereid with tip lying free in an air-lacuna. Note spicules at upper edge of this cell. FIG. 22. Sclereid, showing early stage of secondary wall and pit-canals. Observe the prominent spicules of this cell, some of which extend into air-lacunae. FIGS. 23-26. Transections of sclereids from the cortex of the petiole. FIG. 23. Branched type, showing numerous and closely-spaced pit-canals. FIG. 24. Stellate type, showing pit-canals in the thick secondary wall. FIG. 25. Large, irregularly branched type. Note the conspicuous pit-fields (light areas) in the walls of adjacent parenchyma cells. FIG. 26. Fusiform type, comparable in general form to the cell shown in figure 5. Note the solitary nucleus, the numerous pit-canals and the prominent spicule (upper edge, near center). All figures $\times 190$.



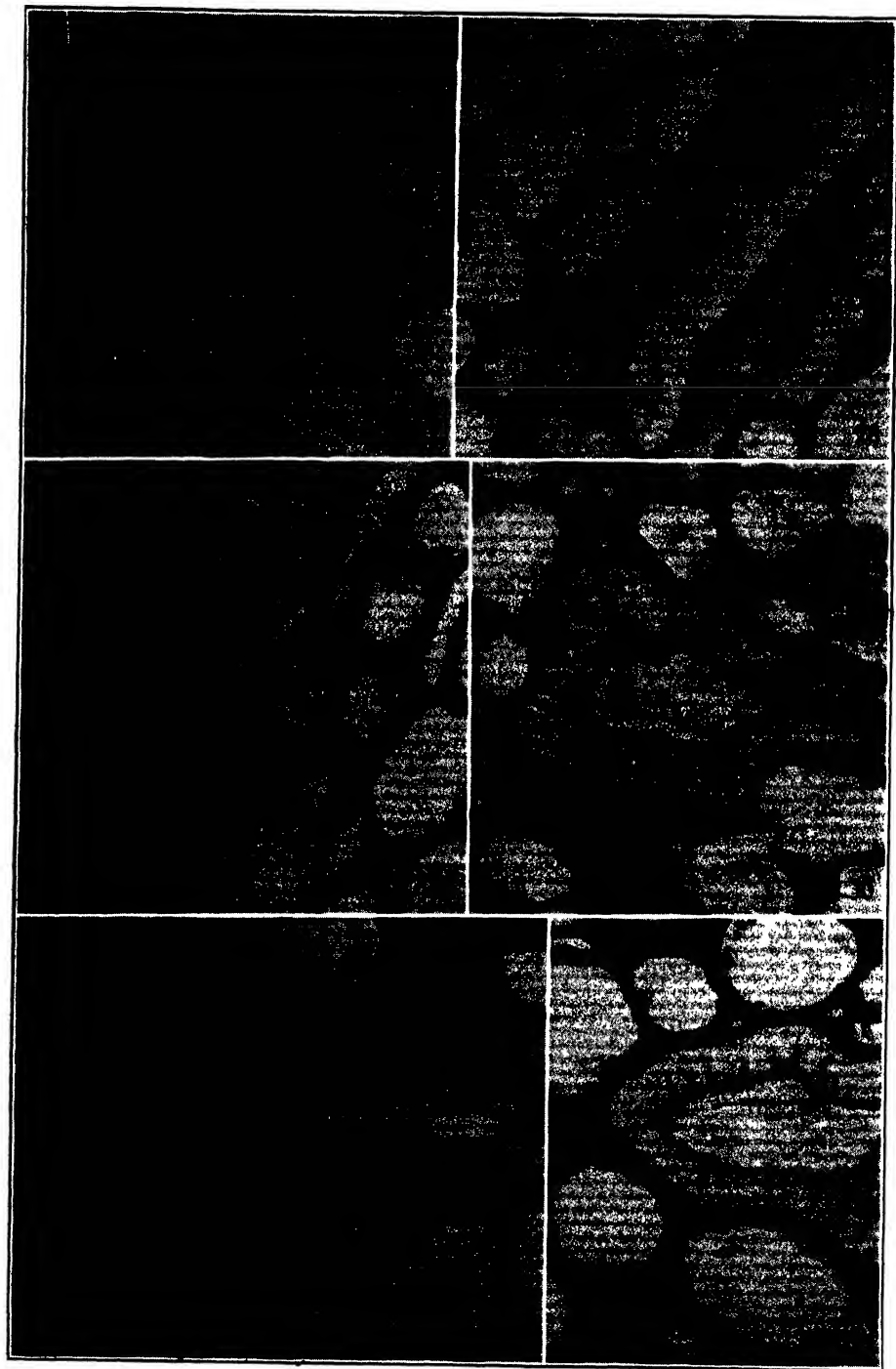
throughout the entire cell. When first recognizable, the young secondary wall is stained a brilliant red with safranin and thus is sharply demarcated from the purplish-blue primary walls of the adjacent parenchyma cells (fig. 18). At this stage, the secondary wall is provided with small shallow pits which are sparsely and unevenly distributed. But as the centripetal deposition of the wall continues, the characteristic pit-canals make their appearance and become increasingly evident and numerous. At maturity, the secondary wall is penetrated by very numerous, slender and often ramified canals which impart a distinctive character to the sclereids of *Camellia* (figs. 19-26).

The investigation of the origin and development of the pit-canals from the simple pits is difficult because the former are so frequently oriented obliquely with reference to the plane of section. As a result, extensive areas of the secondary wall may appear to be traversed by "short" canals which fail to extend to the primary wall of the cell (figs. 23, 26). Furthermore where ramified canals occur, many of the "branches" curve out of the plane of section and thereby produce characteristic effects which are difficult to interpret (figs. 19, 24). It seems clear that the failure to recognize adequately these difficulties is largely responsible for Cavara's (1897, p. 73-74, pl. XXXI, figs. 17-21) description of canal development. He states: "These canals at first are 2.5 microns apart, they are circular in section and .05-.08 microns in diameter. Their arrangement is spiral and very regular, as can be seen in profile. *As the wall thickness increases, the canals increase in number, new ones intercalating themselves between previous ones through new plates of thickening.*" (Italics mine.)

The present investigation furnishes no support for this interpretation. If Cavara's view were correct, the intercalation of new canals between older ones would obviously require some type of centrifugal penetration of the secondary wall by cytoplasmic extensions. Careful examination of young stages provides no evidence for such an assumption. When thin serial sections are compared, it becomes evident that the "new" canals described

Explanation of figures 27-32

Transections of portions of the secondary wall of cortical sclereids to show details of pit-canals. FIG. 27. Young stage in secondary-wall development. A completely-sectioned pit-canal is paired with a primary pit-field at the upper edge of the sclereid. FIG. 28. Section illustrating the oblique course of the canals in the secondary wall. Pairing between pit-fields and pit-canals is shown at left and right near the base of the sclereid. FIG. 29. Illustrating the ramiform pit-canals in a prominent spicule (lower right). Note that a curved canal in the spicule is paired with a pit-field in the adjacent parenchyma cell. FIG. 30. Illustrating ramiform pit-canals (lower edge), and spicules. Two of the canals lie opposite corresponding pit-fields. FIG. 31. Showing two perfectly bisected pit-canals at upper edge of sclereid, and the corresponding pit-fields in the parenchyma cell. FIG. 32. Showing two completely sectioned pit-canals (lower edge). Note the small circular chambers and the pit-membranes. All figures $\times 550$.



by Cavara merely represent the *inner* portion of canals which run obliquely through the entire thickness of the secondary wall. A striking example is furnished by figure 28. At the lower left of the sclereid, the characteristic curved and oblique course of the canals is very evident. Just above this region, a series of four canals may be seen, of which only one extends completely through the wall and coincides with the pit-field of the adjacent parenchyma cell. The other three canals clearly extend at successively more oblique angles, culminating in the short and "incomplete" canal at the top of the series.

Since the sclereids typically develop as idioblasts, the question naturally arises as to the relationship between their very numerous pit-canals and the "sieve pitting"³ on the contiguous walls of parenchymatous elements. As stated earlier in the paper, there is good reason for believing that the intercellular extension of the primary wall of the sclereid results in the splitting apart of certain of the paired primary pit-fields between the parenchyma cells lying in its path. Under such circumstances, one might expect that the pit-canals would coincide in position with some (all?) of the separated members of the originally paired pit-fields. This can be demonstrated in many instances and is not surprising in view of the well-developed character of the sieve-pitting of the parenchyma cells. In figures 27-32, one or more entire pit-canals coincide with primary pit-fields in adjacent parenchyma cells. This relationship is particularly well shown in figures 29 and 32 where the delicate membranes separating the pit-chambers from the pit-fields are clearly seen.

In sectional view, a pit-canal consists of a cone-shaped channel extending from the inner surface of the secondary wall to the small circular pit-chamber. The latter is slightly overarched by the secondary wall and hence may be designated as "bordered" (figs. 27-32).

Extensively "branched" pit-canals develop at various regions of the wall and are particularly well-shown in all of the larger spicules (figs. 19, 21, 22, 26, 29, 30). A study of their ontogeny shows that the "main channel" represents the lateral extension of the lumen into the spicule while the "branches" are a series of originally separate canals which coalesce with the former during secondary-wall thickening. As is shown in figure 19, such ramiform canals are often very complex and difficult to interpret. In the simpler cases, however, it is possible to see that some of the lateral canals are paired with pit-fields in the adjoining parenchyma cell. Often this is associated with a remarkable degree of curvature of the canals (figs. 29-30).

An intensive study of the structure and chemical composition of the sec-

³ This term is used to designate collectively the numerous primary pit-fields with their plasmodesmata which occur in the *primary* walls of parenchyma cells (cf. Bailey and Faull 1934, p. 241-243).

ondary wall of the sclereid has not been attempted. Nevertheless it is noteworthy that throughout its development as well as in its mature condition, the wall appears "homogeneous," i.e., non-stratified. This contrasts markedly with the easily visible lamellae in the secondary wall of the brachysclereids in the fruit of *Pyrus* and the pith of *Hoya carnosa*.⁴ When sections of living petioles of *Camellia japonica* are treated with phloroglucin and hydrochloric acid, the thick walls of the sclereids become red. I-KI produces a bright lemon color. The reaction of the wall to these reagents is suggestive of the presence of "lignin." Cavara (1897) emphasized that as soon as the wall begins to thicken, it assumes a lignified character. His microchemical tests showed that the degree of lignification decreases *inwardly* in the wall, the innermost lamella giving the cellulose reaction with iodine and sulphuric acid. A careful investigation of the physico-chemical make-up of the wall with modern techniques seems highly desirable. This might reveal the presence of non-cellulosic lamellae such as Bailey and Kerr (1935, p. 279-280) have discovered in the walls of sclereids in a number of angiosperms.

DISCUSSION

The present investigation has called attention to the many remarkable aspects of the development, form, and adult structure of the sclereids of *Camellia japonica*. The data may now be discussed most conveniently under two main topics, viz.: (1) the development of the sclereid as an idioblast, and (2) the problem of classifying the sclereid from a morphological standpoint.⁵

Idioblastic Development. Unlike the development of many tissue elements which maintain contacts with *all* their neighbors during differentiation, the ontogeny of the sclereid in *Camellia* involves notable changes in the original intercellular relationships of this cell. Beginning its existence as an idioblast in the parenchyma, the sclereid produces delicate tubular processes which "intrude" into the adjacent tissue and may even extend freely into air-spaces (figs. 9-15). It is very clear that the direction of growth of these tubular branches does not coincide with the short vertical elongation of the petiole. On the contrary, branching occurs in the most varied planes and often is oblique or nearly transverse to the longitudinal files of short parenchyma cells surrounding the sclereid (figs. 13, 14). Evidently, therefore, the extension of the sclereid is not explainable in terms of

⁴ Buch (1870, p. 17) observed that the thick walls of the elaborately branched sclerenchyma cells of *Fagraea auriculata* exhibit a clearly laminated structure. The writer was able to confirm this observation in a study of macerated elements of a petiole of *Fagraea* secured from the herbarium of the University of California.

⁵ The writer acknowledges with thanks the many helpful discussions on "sclerenchyma" with Professor I. W. Bailey.

Priestley's (1930) theory of "symplastic growth." For this reason and also because there is no evidence of intracellular growth by the ramifying sclereid, it seems clear that true intercellular development must occur.

Although this conclusion appears inescapable, many difficulties arise when one attempts to visualize the "mechanics" of this type of idioblastic development. Does a considerable portion of a tubular branch of a young sclereid literally "glide" or "slip" over the walls between two neighboring protoplasts? Or, is elongation strictly limited to the very tips of the sclereid branches?

The latter type of growth movement in plant cells has been termed "intrusive growth" by Sinnott and Bloch (1939), who consider that true sliding growth "is rare or absent in most plant tissue and cannot be regarded as an important factor in development." Majumdar (1941, p. 170) reaches an essentially similar conclusion with respect to the fusiform initials of cambia and certain fibers. In their recent study of the development of the fibrous net in *Luffa cylindrica*, Sinnott and Bloch (1943, p. 98) state: "That the growth of the *Luffa* fibers is chiefly at their ends is indicated by the much thinner walls there. The two halves of a pit are always opposite each other, showing that there is no gliding after the pits are formed."

Because of the limitations of present technique, it is apparent that the evidence in favor of either "gliding growth" or "intrusive growth" is necessarily indirect. This will be true until methods have been devised for the direct observation of internal differentiating cells. Furthermore, the distinction between these two types of growth movements appears to be one of degree rather than of kind. For example, it seems clear from Bailey's (1923, p. 502-505) investigations that rather extensive wall elongation occurs during the increase in girth of non-stratified cambia. In such tissue, according to Bailey "the fusiform initials elongate, sliding by one another, until they attain a certain size." In contrast the fusiform initials of stratified cambia "divide radio-longitudinally and the products of such divisions expand laterally, but they do not elongate to any considerable extent." These differences in the degree of intercellular growth of cambial initials seem analogous to the various degrees of branching of the sclereids in *Camellia*. In the development of the "major branches" of a sclereid, elongation of considerable portions of the primary wall seems entirely possible. On the other hand, the growth of the characteristic spicules is more limited and very probably represents "intrusive growth." Vöchting (1908), in his classical treatise on morphogenesis, paid much attention to the bizarre types of idioblastic sclereids which were produced in great abundance in the tumors on leaf-bases of kohlrabi. With reference to the development of the sclereids Vöchting states (p. 192): "It is without further explanation clear that the penetration of the processes between the neighboring cells can only

be visualized by means of 'gliding' growth, which, as one sees in our tumors as well as in wound-tissue and other places in the plant, is of wide distribution." (Cf. also Küster 1935, p. 553-554.)

Whether the branched sclereids in *Camellia* are produced by "sliding" or "intrusive" growth, it seems evident that some of the original pairs of pit-fields, with their protoplasmic connections (or contacts) must be split apart. As discussed earlier in this paper, the slender and often ramified pit-canals of the sclereid are laid down opposite certain of the separated pit-fields of adjacent parenchyma elements (figs. 27-32). It has not been possible, however, to determine the effects of intercellular growth upon the middle lamella through which the tubular branches must penetrate. Since Kerr and Bailey (1934) have shown that the middle lamella is amorphous and plastic in character in young tissue, it is possible that the tubes "digest" their way between cells by the secretion of enzymes which act both chemically and physically upon polyuronides (cf. Paton 1921). This possibility of course needs to be tested experimentally.

Morphology of the Sclereid. The difficulties which arise in any attempt to classify morphologically the varied cell types in plants have been discussed recently by the writer (Foster 1942, p. 32-43). While it is relatively easy to demarcate the extremes in cellular specialization, frequent intergradations in form, wall structure, pitting, etc., occur and preclude rigid categories. The cells considered in this paper furnish a good illustration of the problems, because eleven more or less distinct terms have been applied to them since their discovery (table 1). When the various terms are examined

TABLE 1. *Summary of the terms which have been used in attempting to classify morphologically the branched cells in the leaf of Camellia.*

All authors in this table are listed under "Literature Cited."

Term	Originator	Applied to branched cells of <i>Camellia</i> leaf by
Fibers	?	Mirbel and Payen (1849, 1850); DeBary (1884); Dippel (1898)
Sclerenchyma cells	Mettenius (1865)	Mettenius (1865); Buch (1870); Wiesner (1890); Palladin (1914)
Bast cells	?	Hofmeister (1867)
Idioblasts	Sachs (1874)	Cavara (1897); Kochs (1900); Solcreder (1908)
Trichoblasts	Sachs (1882)	Sachs (1882); Luerssen (1893)
Sclereids	Tschirch (1885)	Melchior (1925); Puchinger (1923)
Astrosclereids	Tschirch (1885)	Tschirch (1885, 1889); Haberlandt (1914); Jackson (1916); Küster (1935); Foster (1942)
Bast fibers	?	Goodale (1885)
Stone cells	?	Schumann (1889); Warming-Johansen (1909)
Stereocytes	Chodat (1920)	Chodat (1920)
Sclerites	Seward (1906)	Beauvisage (1920)

from an historical standpoint, it at once becomes clear that much of the confusion has arisen from (1) the gradual modification of Mettenius's (1865) concept of "sclerenchyma," and (2) the strong influence of Schwendener's (1874) physiological classification of "mechanical elements."

TABLE 2. *Diagram showing the main steps in the historical development of the concepts of "sclerenchyma" and "stereome."*

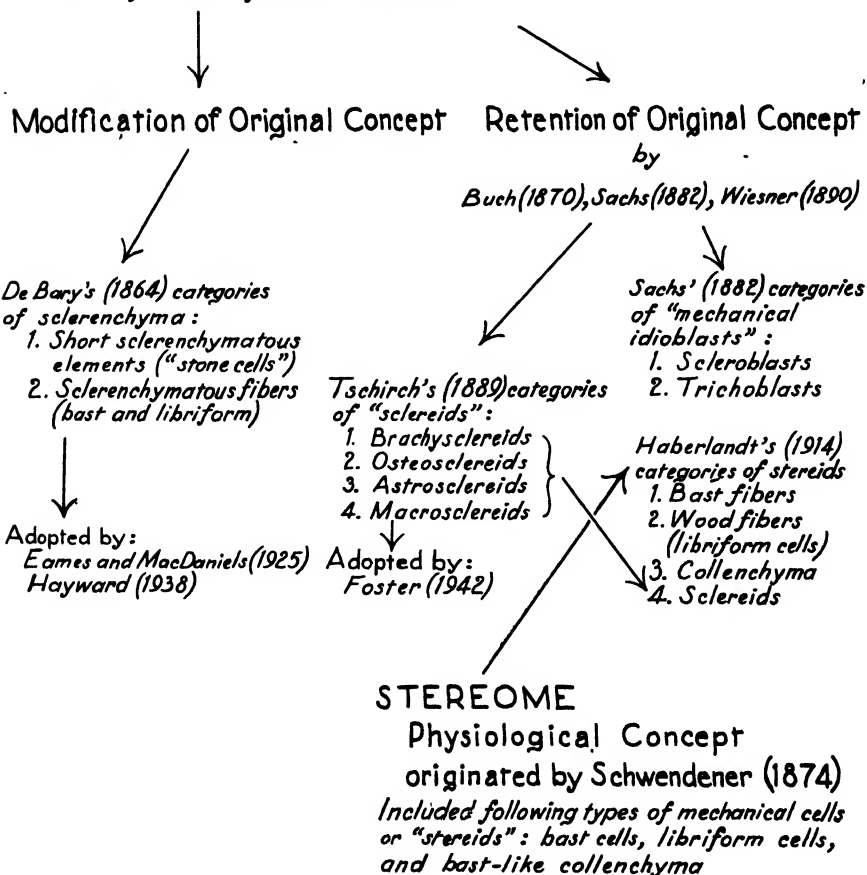
All authors in this table are listed under "Literature Cited."

SCLERENCHYMA

Morphological Concept

originated by Mettenius (1865)

*Included: thick-walled parenchyma and prosenchyma
exclusive of "bast" of vascular bundles*



As is shown in table 2, the concept of sclerenchyma as originally defined by Mettenius (1865) included thick-walled "parenchyma" and "prosenchyma" *exclusive* of the bast fibers of the vascular system. Buch (1870, p. 16) accepted this idea and emphasized that his concept of "sclerenchyma cells" included "all strongly thickened cells lying outside the vascular bundle, regardless of the ultimate form of the cell." Mettenius cited as an example of sclerenchyma cells the isolated thick-walled elements in the petiole of *Camellia*, and his viewpoint was later adopted by Buch (1870), Wiesner (1890), and Palladin (1914). Sachs (1882) likewise accepted Mettenius's concept of sclerenchyma and proposed the terms "scleroblast" and "trichoblast" for sclerenchymatous idioblasts which do not form a true tissue. Under "trichoblasts," Sachs included the branched cells in *Camellia* leaves as well as the "internal hairs" of *Nuphar* and *Monstera*. Reference to table 1 will show that Sachs' more general term "idioblast" has been preferred by a number of writers, although when used in this sense for the branched cells of *Camellia* it is entirely noncommittal in a morphological sense.

Strongly influenced by the physiological ideas of Schwendener, Tschirch (1885, 1889) proposed the term "sclereid" for a class of thick-walled "mechanical cells" which he believed are distinct in form and wall-structure from "bast cells" (i.e., bast fibers). His categories of sclereids (cf. table 2) are based principally upon the *form* of the cell and include idioblastic types (i.e., "osteosclereids" and "astrosclereids") as well as tissue-forming types (i.e., "brachysclereids" and "macrosclereids"). The term sclereid, because it is brief and etymologically clear, has much to commend it and hence has been adopted in this paper and in the writer's recent book (Foster 1942, p. 67-72). As is shown in tables 1 and 2, it has been applied to the branched cells of *Camellia* by Melchior (1925) and Puchinger (1923), and is used by Haberlandt (1914, p. 158) to designate one of the four main types of "stereids."⁶

Beginning with DeBary's (1884) classic text, the original concept of sclerenchyma was broadened to include bast and libriform fibers as well as "short" sclerenchymatous elements (e.g., "stone cells"). Unfortunately this did not lead to any general agreement on the most appropriate classification of the branched cells in *Camellia*. DeBary (1884), Goodale (1885), and Dippel (1898) regarded these cells as "fibers," while Schumann (1889) and Warming-Johansen (1909) designated them as "stone cells." Chodat (1920) likewise interpreted the cells as fibers and his special term "stereo-

⁶ It will be noted from table 2 that Haberlandt recognizes collenchyma as a category coordinate with fibers and sclereids. Since "typical" collenchyma cells develop only primary walls (Esau 1936) and are capable of growth and division even when mature, Haberlandt's classification is open to criticism, at least from a morphological standpoint.

cytes" reflects the additional influence of Schwendener (cf. table 2). The term "sclerites" is not obviously related either to the concept of "sclerenchyma" or "stereome." It was applied by Seward (1906) to the branched idioblasts found in the leaves of *Araucaria* and *Agathis* and was employed in a similar way for the branched cells of *Camellia* by Beauvisage (1920) in his monograph on the *Ternstroemiaceae*.

From the historical analysis just given and in the light of the present investigation, it is evident that the whole concept of sclerenchyma merits careful re-examination. Solereder (1908, p. 1091-1092) lists 84 families of dicotyledons in which idioblastic "sclerenchyma" cells occur in the mesophyll of the leaf. He rather loosely terms all such elements "spicular cells," apparently adopting the term from Hooker's (1864) designation of the remarkable crystal-bearing cells found in *Welwitschia*. According to Matsuda (1894, p. 128; pl. IV, fig. 20) crystal-bearing sclerenchyma cells, essentially similar to those of *Welwitschia*, occur in the dicotyledon *Kadsura japonica*. The need for broad comparative studies is thus very clear. They should include investigations not only on cell development but also on the structure and chemical make-up of the secondary wall. Important advances in this direction have already been made on fibers of various types by Bailey and Kerr (1935) and Esau (1938, 1943). When more data are available, it may be possible to differentiate more scientifically a series of categories under "sclerenchyma." It seems clear that both fibers and sclereids of various types would occur in any morphological classification of this kind.

Postscript. After completing the entire manuscript for this paper, the writer "discovered" a much-neglected treatise on the comparative morphology and functions of sclereids in seed plants. This remarkable work, consisting of 96 pages of text and 3 plates, was written in 1890 by C. J. Wijnaendts Francken and appeared as a printed dissertation from Utrecht University under the title of "De Sclereïden." The fact that this dissertation was not subsequently published in a scientific journal doubtless explains why it has not been more widely noted in histological literature. Apparently the only previous allusion to it is by Solereder (1908), who includes it among the literature "references" under certain dicotyledonous families. With the indispensable aid in translation given by the writer's colleague, Dr. George F. Papenfuss, it is evident that "De Sclereïden" is monographic in scope. It includes not only a description of sclereid morphology in seed plants (14 genera of gymnosperms and representatives of 14 families of angiosperms are considered) but it also attempts to review critically the problems of terminology and classification of the varied forms of idioblastic sclereids from much the same standpoint which has been adopted by the present writer. Wijnaendts Francken was evidently strongly influenced by the ideas of Schwendener, Tschirch, and Haberlandt, as is shown

by his effort to demarcate sharply between "bast fibers" and "sclereids." While recognizing that intergradations occur between these two cell types, he concludes that sufficient differences exist to justify separate terms for them. He also emphasizes that although sclereids usually originate from "ground tissue" cells, their distribution within organs is so varied that they cannot be regarded as a "unity" either ontogenetically or phylogenetically. As regards the Ternstroemiaceae, he investigated the sclereids of *Camellia japonica*, *C. sasangua*, *Thea viridis*, and *T. Bohca*. In *Camellia* he was unable to detect, even by using reagents, any lamellae in the secondary wall and he described the latter as "homogeneous." This observation is supported by the present investigation. Space does not permit further discussion, but the writer desires to emphasize his belief that "De Sclereiden" deserves the attention of modern workers and should serve as a valuable orientation for the much-needed comparative investigations on sclereids in seed plants.

SUMMARY

This paper describes a study of the structure and development of the sclereids in the petiole of *Camellia japonica*.

The sclereids occur as typical idioblasts distributed in the parenchyma of "cortex" and "pith." When isolated by maceration, the adult sclereids are remarkably polymorphic cells, ranging in shape from fusiform types to elaborately ramified elements. In all form-types, more or less numerous, short, conical or irregular protuberances are characteristic. These protuberances are termed "spicules" and their occurrence on the petiolar sclereids of *C. reticulata* and *C. sinensis* is noted.

Sclereids originate from parenchymatous cells of the cortex and pith of the petiole during the final phase of enlargement of the foliage leaf. The initial cells, despite their idioblastic distribution, can be identified by their greatly enlarged nuclei. During the earliest stages of development, the sclereid initial produces one or more delicate tubular branches which extend between the walls of neighboring tissue-elements and may ultimately penetrate certain of the intercellular air-spaces. The continued ramification of the sclereid is accompanied by the origin and development of "spicules" which, like the major branches, grow in between the walls of adjacent parenchyma cells. Throughout the life of the sclereid, the protoplast remains uninucleate.

When the sclereid has completed its intercellular development, a massive secondary wall, traversed by slender and often ramiform pit-canals, is produced. A pit-canal consists of a cone-shaped channel extending from the lumen to the small circular chamber. The latter is slightly overarched by the secondary wall and is paired with a pit-field in the wall of the adjacent parenchyma cell.

The intercellular development of the sclereid is discussed with reference to the theories of "gliding" and "intrusive" growth. While the latter type of growth probably occurs during spicule development, the elongation of the major branches is not necessarily restricted to their tips.

The problem of classifying the sclereids of *Camellia* morphologically is discussed and the confused terminology is examined in the light of the historical development of the concepts of "sclerenchyma" and "stereome." The need for comparative studies on the development and wall structure of sclerenchymatous cells is emphasized.

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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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PLANT TAXONOMY AND FLORISTICS

(exclusive of fungi)

(See also under Genetics: **Babcock & Jenkins**)

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THE FUNCTION AND STRUCTURE OF THE PARENCHYMA SHEATH PLASTIDS OF THE MAIZE LEAF

M. M. RHOADES AND ALCIDES CARVALHO¹

In connection with a genetic study of chlorophyll variegation in maize (Rhoades 1943) it was necessary to prepare sectioned material of the leaf. When these slides were examined, our attention was caught by the unusual plastids of the single-layered parenchyma or bundle sheath cells surrounding the vascular bundles. A survey of the literature disclosed no account of these plastids which agreed with our conception of their structure and function; so a brief account has been prepared.

Many grasses have two cell layers surrounding the vascular bundles, while others have a single layer. Schwendener (1890) designated the outer layer as the parenchyma sheath and the inner layer, whose inner walls are often thickened, as the mestome sheath. The parenchyma sheath cells of some grasses contain chloroplasts, while these cells of other grasses are colorless. The members of the subfamily Pooideae have the vascular bundles enclosed in a thick-walled mestome sheath surrounded by a parenchyma sheath, while in the subfamily Panicoideae there is only a parenchyma sheath (Arber 1934). That the cells of the parenchyma sheath of many grasses contain chloroplasts has long been known, and their presence led Haberlandt (1914) to suggest that the green parenchyma sheath cells might have an undiscovered function in addition to their acting both as the efferent tissue and as an unimportant addition to the chlorophyll-apparatus of the plant. Although this question posed by Haberlandt has been answered in part, it is the purpose of this paper to present further studies on the structure and function of the chloroplasts in the parenchyma sheath cells of the maize leaf.

Schwendener (1890) and Strasburger (1891) reported that the parenchyma sheath enclosing the vascular bundle of the maize leaf was chlorophyll-bearing. Kiesselbach (1916) observed that the parenchyma sheath cells of maize contained chloroplasts larger than those of the mesophyll cells. He further stated that these plastids "assumed an abnormal elongated shape and grouped themselves in an unnatural crescent arrangement about the outer edge of the cells" when subjected to a chrome-acetic fixing agent. Weatherwax (1923) mentions the large prominent chloroplasts of the parenchyma sheath but adds nothing to Kiesselbach's observations.

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Eames and MacDaniels (1925) figure a cross section of a corn leaf which gives a misleading picture of the parenchyma sheath plastids. They also identify the parenchyma sheath of grasses as the mestome sheath, which is contrary to the terminology of other investigators. Avery (1930) also figured and briefly described the parenchyma sheath of the leaf bundles of maize and stated: "The vascular bundles are surrounded by a chlorophyll-bearing bundle sheath. The chloroplasts of the bundle sheath cells differ from those of other cells of the leaf." Arber (1934) figures a cross section of a leaf bundle of maize showing the parenchyma sheath but makes no statement about the plastids. Sharman (1942) and Esau (1943) have made careful studies on the ontogeny of the vascular bundles of maize. Esau noted that the parenchyma sheath cells contained abundant large chloroplasts, while Sharman made no mention of the plastids. The papers cited above may be summarized, in so far as they concern the parenchyma sheath, as agreeing only that the single layer of cells comprising the parenchyma sheath around the vascular bundles in the maize leaf contains numerous chloroplasts larger than those of the mesophyll cells.

Zirkle (1929) in an intensive study of the plastids of maize recognized that the cells of the bundle sheath contained specialized chloroplasts concerned with starch storage. He believed that the smaller plastids of the mesophyll had central vacuoles containing starch when conditions were favorable for photosynthesis. Each plastid of the bundle sheath cells was thought to contain in the plastid vacuole a centrally located starch grain. According to Zirkle, the surfaces of these plastids possess pores leading to their central vacuoles. When the plastids were oriented on their flat surfaces, the pores appeared round, but when the plastids were viewed from the side they appeared as slits. He concludes that the pores are concentrated on the flatter surfaces of the plastid and lead to the vacuole but do not point to the plastid's center. We believe that Zirkle has misinterpreted several important structures. Further reference to his account of these plastids will be made later.

Weier (1932), in a paper dealing with the possible homology of the plastids with the Golgi zone, figured a cell from a maize leaf which unquestionably came from the parenchyma sheath, although Weier does not so state. He found that the plastids of this cell contained "cavities" filled with starch. He says nothing of the kinds of chloroplasts found in the mesophyll and bundle sheath cells.

STRUCTURE OF THE BUNDLE SHEATH PLASTID

A brief survey of the voluminous but controversial literature on plastid structure reveals that their fixation images may differ greatly from their appearance in living cells. Since most of our observations were made on

fixed material, it is clear that our comments on the structure of the parenchyma sheath plastids must remain of a tentative nature until a more thorough study has been made. However, some of the grosser features are clearly revealed, and it is with these that we shall concern ourselves.

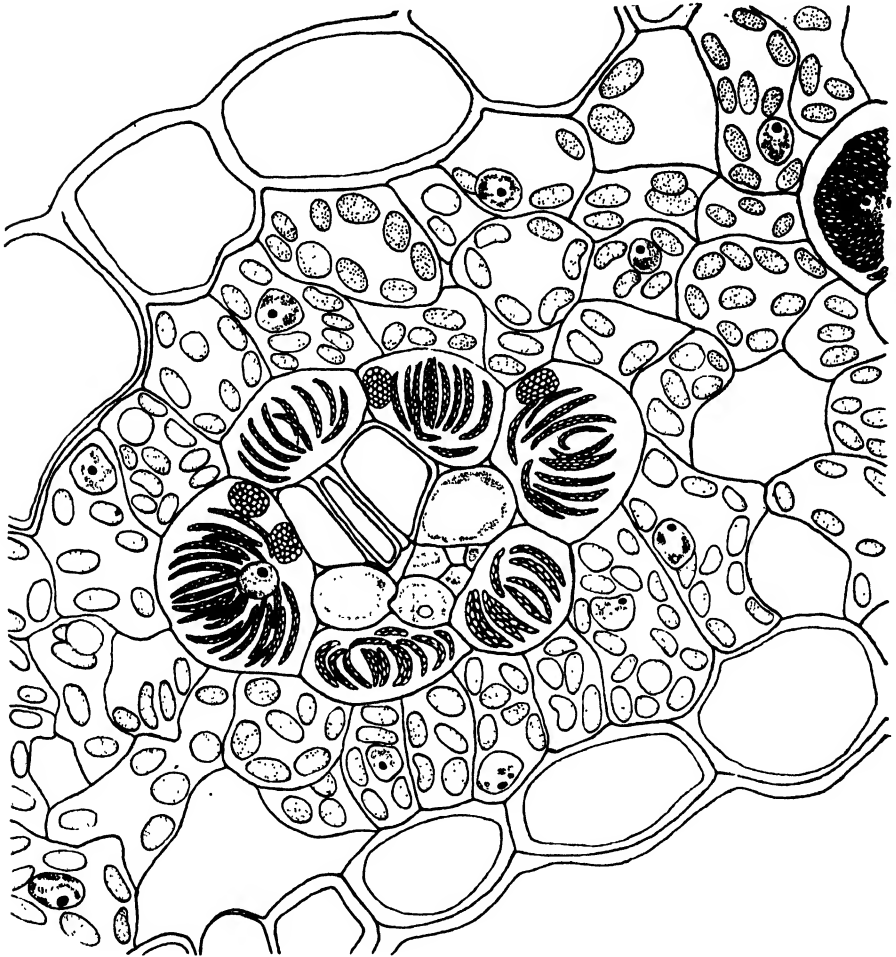


FIG. 1. Cross section of a maize leaf showing single-layered parenchyma sheath enclosing vascular bundle containing flattened ellipsoidal starch-containing plastids. Most of the plastids in the sheath cells are so oriented that a cross section of the leaf presents them in side view, but a few are shown in face view. The sheath cells contained many more plastids than are included in the drawing; in some cells they were tightly packed like a stack of coins. In side views of the plastids the starch grains appear as small ellipsoidal bodies, while in face views they have a spherical shape.

Kiesselbach (1916) found a marked difference in appearance between fixed and living bundle sheath plastids of corn. He believed that the fixing

fluid caused the plastids to assume an unusual crescent-like orientation in the cell. Our own observations, however, indicate that except for changes in position due to alterations in the size and shape of the plastids, it is doubtful if any movement of these plastids occurs upon their being fixed. When free-hand sections of fresh leaves were mounted in water, the plastids absorbed water and became distended. Fixation images of these plastids were very similar when fixed in Regaud's, Champy's, or Craf; their fixed appearance resembled that of living material mounted in paraffine oil.

In fixed material stained with haematoxylin the plastid of the bundle sheath appears as a flattened ellipsoid with a deeper-staining rim or shell partially enclosing a lighter-staining central core (figs. 1, 3, 6, 8). When viewed from different positions, these plastids present varying shapes owing to their asymmetrical form. Bundle sheath plastids, especially those which lack starch grains, in face views have a striking resemblance to the dictyosomes of the Golgi apparatus. The peripheral, more deeply staining rim is seen to contain in starch-free plastids numerous small colorless areas which appear like vacuoles. It is in these vacuolar-like regions of the plastid that starch is later deposited. The "vacuoles" and the starch grains have the same shape and approximate size. When starch is present, the grains are found embedded in but protruding from the surface of the plastid. The central region of the plastid contains neither starch vacuoles nor starch grains. The number of starch-forming "vacuoles" in a starch-free plastid may be equal to the number of starch grains subsequently formed by that plastid. It is possible, however, that as soon as one of these "vacuoles" has formed one mature starch grain, it begins the elaboration of a second, and so forth, so that the number of starch grains formed may be greater than the number of starch-forming regions. A decisive answer to this problem could be had either by an accurate determination of the number of "vacuoles" in a living plastid and the number of starch grains found later or by a statistical study of fixed material. In a single plastid the starch grains, which are arranged in several layers when viewed on edge, range in number from fewer than 20 to more than 40. The individual starch grains are easily detached from the surface of the plastid and may be found floating free in the mounting fluid. These detached grains are especially noticeable in iodine-stained preparations, where they appear as blue-colored ellipsoidal bodies. Although a plastid contains a number of starch grains, each grain is simple rather than compound. Figure 2 is an optical section of a young plastid containing 20 individual starch grains. Ten of the grains lie in one focal plane, the remainder lying above and below. These definite regions, the vacuoles, of the parenchyma sheath plastid which are concerned with starch formation are similar in function, though not in structure, to the pyrenoids of algal and moss plastids.

A comparable situation has been reported by Zirkle (1926) for the ordinary (mesophyll) plastid of *Elodea canadensis* which has a central vacuole containing a single starch grain. This vacuole is visible when no starch is present.

The parenchyma sheath cells enclosing young vascular bundles of maize have smaller plastids than do older cells; they not only have fewer starch grains but are less flattened than plastids of mature bundles.

The above description of the parenchyma sheath plastid differs in several fundamental respects from Zirkle's (1929) account. What he believes to be pores of the plastid leading to the centrally located vacuole are actually starch grains, which do not stain with haematoxylin and appear colorless

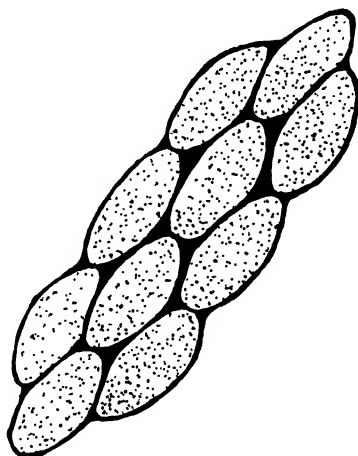


FIG. 2. Median optical section of a small parenchyma sheath plastid in side view showing arrangement of starch grains. These starch grains are embedded in the plastid but are separated from each other by thin layers of plastid substance. This plastid contains 20 starch grains. Ten are in one focal plane, the remainder lying above and below. The central region of the plastid is not visible when viewed from this position. This plastid is a much less flattened ellipsoid than those shown in figure 1.

(see Zirkle's figure 1). He believes that each plastid contains a single centrally located starch grain; but we have shown that these plastids have as high as 40 starch grains. Zirkle reported that the mesophyll plastids contained starch in their central vacuoles when conditions were especially favorable for photosynthesis. In our experiments with field-grown maize we found no trace of starch in these plastids either with the iodine test or with polarized light. This was true even though abundant starch was present in the bundle sheath plastids. We conclude that starch synthesis normally does not occur in the mesophyll plastids; they are devoted to the elaboration of soluble carbohydrates. That the differences in structure and function between the mesophyll and sheath plastids may be only a reflection of local

physiological conditions, especially the concentration of soluble sugars, and are not due to inherent differences is indicated by the observation of the remarkable transformation of the mesophyll plastids into sheath-like plastids by greatly increasing the amount of sugar present in the leaf. The cut ends of young maize leaves were immersed in a strong sucrose solution (27 grams of sucrose in 100 cc. of water). After 30 hours in the sugar solution the mesophyll plastids in the portion of the leaf just above the level of the solution each contained a number of simple starch grains. Seventy-eight hours after being placed in the sugar solution the change of the mesophyll plastids into sheath-like plastids was virtually complete. Except that the smaller mesophyll plastids contained fewer but larger starch grains they closely resembled the sheath plastids. In normally growing leaves the sugars manufactured in the mesophyll cells are moved into the bundle sheath cells. Presumably the sugar concentration of the mesophyll cells remains at a relatively low level while that of the bundle sheath becomes increasingly greater. Under such conditions the mesophyll plastids are concerned only with photosynthetic activity while the bundle sheath plastids elaborate, and temporarily store, starch. However if the sugar concentration of the mesophyll cells becomes unusually high it might be expected, on the basis of the above experiment, that the mesophyll plastids would contain starch.

It has long been known that the plastids of the bundle sheath cells of the corn leaf are green, although of a lighter color than the plastids of the mesophyll. If the green pigment is chlorophyll, these plastids may be capable of photosynthesis. The starch deposited within them might be derived from sugars synthesized there and not from soluble carbohydrates moved in from the surrounding mesophyll cells. The heavy deposit of starch found in these plastids would seem to be greater than could be accounted for by their photosynthetic activity, but actually nothing is known of their ability in this respect. Fortunately we were able to show unequivocally that the starch found in these plastids was derived from soluble carbohydrates made in the mesophyll plastids and translocated to the parenchyma sheath cells where the starch synthesis occurred. Certain of the maize leaves collected for study were green-and-white-striped. The plastids in the white regions were quite distinct from the normal plastids in the green area of the leaf (Rhoades 1943). At the transition zone between the green and white regions of one leaf a vascular bundle was found enclosed by parenchyma sheath cells with normal plastids. Adjacent to the sheath cells on one side of the bundle were mesophyll cells with normal green plastids, while next to the remaining sheath cells were mesophyll cells with abnormal plastids which lack chlorophyll and are incapable of photosynthesis. The plastids of the sheath cells touching green mesophyll cells were filled with starch grains, while the normal plastids of bundle sheath cells adjacent to colorless meso-

phyll cells contained no detectable starch. Not answered by this experiment is the question whether or not any photosynthesis takes place in the green bundle sheath plastids. A certain amount of sugar could be manufactured, but if the concentration were low, it could be immediately moved into the vascular bundle.

It has been tacitly assumed that the pale green color of the bundle sheath plastids is that of chlorophyll. Zirkle (1926) noted the lighter color of the sheath plastids of *Elodea* and suggested that they contained as much chlorophyll as the smaller mesophyll plastids but that it was stretched into a thinner layer in the larger sheath plastids. The question might be left open as to whether or not the green pigment in the bundle sheath plastids is the same kind of chlorophyll as in the mesophyll plastids. It has been shown that there is wide variation in the chlorophyll pigments throughout the plant kingdom. For example, Spoehr *et al.* (1942) have shown that certain algae lack chlorophyll b while containing chlorofucine. The possibility should not be summarily dismissed that even within an individual plant there may be variation in the kind of chlorophyll or in the ratio of chlorophyll a to chlorophyll b in different cells. Sayre (1926) found that the guard cells of *Rumex patientia* contained a green pigment which he believed on the basis of microchemical tests was not true chlorophyll. Since the bundle sheath plastid of the corn leaf differs from the mesophyll plastid in function and structure, the nature of their green pigments might not be identical.

DIURNAL CYCLE OF STARCH FORMATION BY BUNDLE SHEATH PLASTIDS

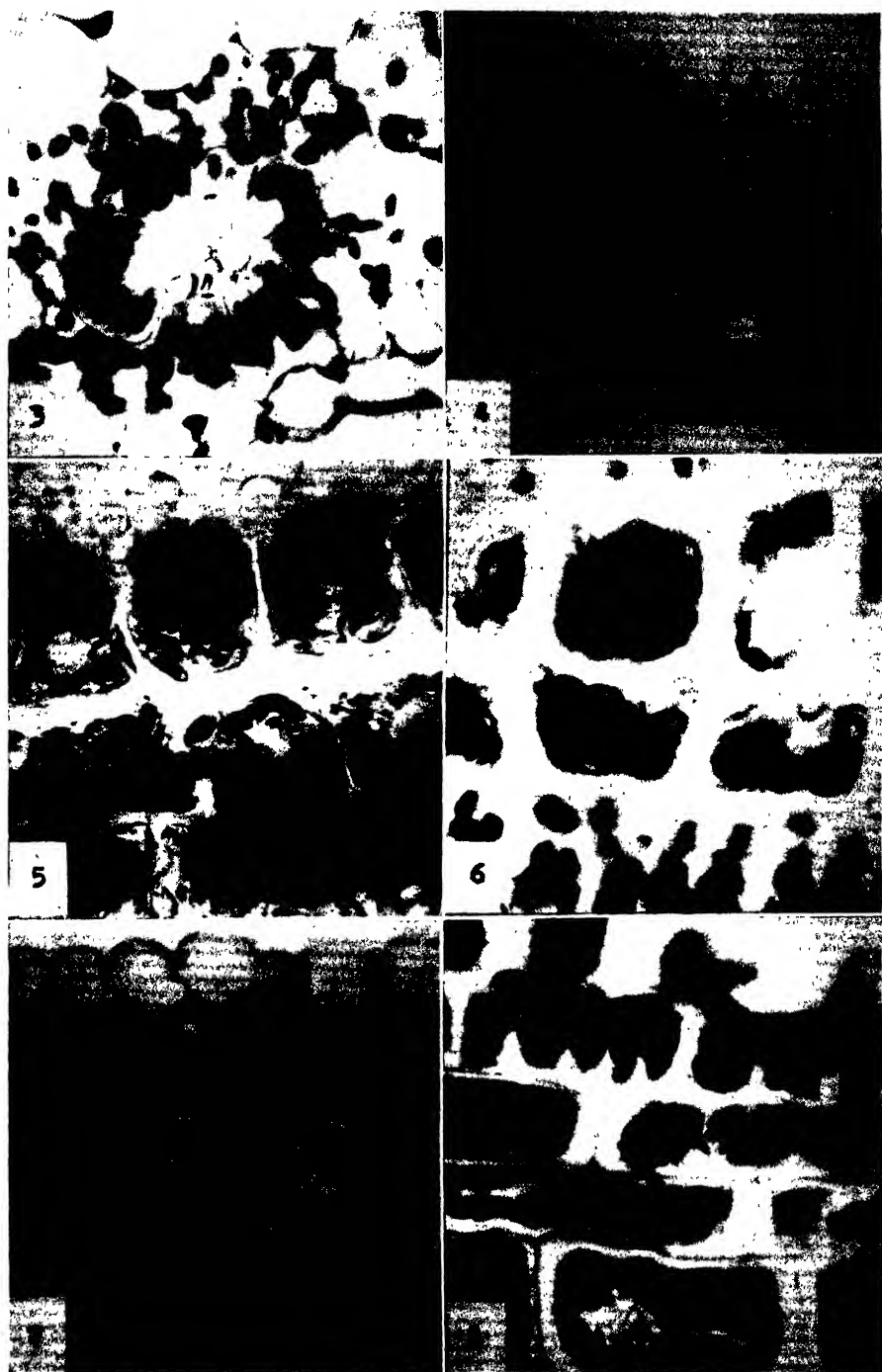
We have presented evidence that the starch deposited in the bundle sheath plastids comes from soluble carbohydrates made in the mesophyll cells and moved into the sheath cells where the transformation to starch occurred. In this section experiments are discussed which indicate that the transformation of soluble carbohydrates to starch occurs in the bundle sheath plastids only when the rate of movement of sugar into these sheath cells from the mesophyll cells is greater than the rate of translocation from the bundle sheath cells into the vascular bundles. Further, we shall show that the starch which increasingly accumulates throughout the day in these plastids is transformed back to soluble carbohydrates during the night, when no photosynthetic activity takes place, so that by morning the bundle sheath plastids are devoid of starch.

Leaf samples were taken approximately 6 inches from the tip of mature leaves from each of three plants at two-hour intervals beginning at 6:30 a.m. Eastern War Time on July 27, 1943, and ending at 12:30 a.m. on July 28. At 6:30 a.m. on July 28 another collection was taken from each of the three plants. Each sample consisted of a piece of leaf blade 2 cm. long and

1.5 cm. wide. Two samples only were taken from a single leaf; they came from opposite sides of the midrib and in all cases were collected at successive time intervals. Samples were taken only from the upper leaves of the main stalk or of the several tillers, where leaves were well exposed to the rays of the sun. Conditions were presumably excellent for photosynthesis, since the day was warm and there was an adequate supply of moisture in the soil. The leaf samples were fixed in Craff fluid. Some slides were stained with haematoxylin and some with a weak I-KI solution. Preliminary tests had shown that the bundle sheath plastids seemed devoid of starch when leaf samples were taken in the morning, while abundant starch was found later in the day. The leaf samples collected at 6:30 a.m., July 27, had bundle sheath plastids with no or little starch. In only an occasional sheath cell could starch be detected by I-KI. The 8:30 a.m. samples were completely devoid of starch; all starch present in these plastids had been hydrolyzed and translocated. Starch grains were found in the 10:30 a.m. samples but in a relatively slight amount as indicated by the intensity of their blue color with I-KI. The 12:30 p.m. samples had a markedly greater amount of starch. Plump starch grains protruded from the surface of the sheath plastids and gave an intense color with I-KI. All three of the 2:30 p.m. samples gave a weaker color with I-KI, indicating that less starch was present than at 12:30 p.m. This finding is important in view of the fact that the morning of July 27 was clear and bright. Beginning approximately at 1:00 p.m. and lasting until about 3:00 p.m., the sky became heavily overcast and the light intensity was greatly reduced. Presumably less photosynthetic activity occurred in the mesophyll cells during the overcast period; less sugar was passed into the bundle sheath cells than was moved into the vascular tissues.

Explanation of figures 3-8

FIG. 3. Cross section of maize leaf collected at 4:30 p.m., showing plastids of parenchyma sheath cells filled with starch grains. Fixed in Craff fluid; stained with haematoxylin. $\times 480$. FIG. 4. Longitudinal section of maize leaf stained with weak I-KI. Starch grains in parenchyma sheath plastids deeply stained. Mesophyll plastids (above and below parenchyma sheath) give no indication of starch. Note starch in guard cells at lower right (slightly out of focus). $\times 480$. FIG. 5. Longitudinal section of maize leaf stained with I-KI followed by partial removal of iodine with higher alcohols. The starch grains are clearly visible in the somewhat swollen plastids. $\times 480$. FIG. 6. Longitudinal section of maize leaf collected at 6:30 a.m. Fixed with Craff fluid and stained with haematoxylin. Parenchyma sheath plastids are devoid of starch. Mesophyll cells lie to right. The deeper-staining rim or shell which partially encloses the lighter-staining central core is clearly visible in certain of the plastids. The vacuole-like regions of the deeper-staining rim where starch grains will be formed can be seen as light-staining regions. $\times 480$. FIG. 7. Cross section of barley leaf showing parenchyma sheath cells with small plastids concentrated to one side of cell. These plastids take a deeper stain with haematoxylin than do the larger plastids of the mesophyll cells. $\times 360$. FIG. 8. Longitudinal section of maize leaf collected at 6:30 a.m. Stained with haematoxylin. When seen in face view the sheath plastids resemble the dictyosomes of the Golgi apparatus. Note vacuole-like regions in deeper-staining rim of plastid. $\times 480$.



so part of the starch accumulated by the sheath plastids in the late morning hours was hydrolyzed to soluble sugars and translocated. The skies cleared about 3:00 p.m. and the rest of the day was sunny and bright. The 4:30 p.m. samples contained a great quantity of starch, as did the 6:30, 8:30, and 10:30 p.m. samples. It is our impression that the greatest quantity of starch was present in the 6:30 and 8:30 p.m. samples, but no quantitative determinations were made.

The sun set at 8:18 p.m. on July 27. There was still a considerable amount of starch in the bundle sheath plastids of the samples collected at 12:30 the following morning but less than at 10:30 the night before. It was possible to find a few plastids with a faint blue color in the 6:30 a.m., July 28, samples, but the majority of the bundle sheath plastids gave no indication of starch with I-KI. All or nearly all of the starch formed in these plastids in the daylight hours of July 27 had been transformed back to sugar during the night.

The sun rose at 5:46 a.m. on July 27. It was a warm and sunny morning. A minor but detectable quantity of starch could be found in a few of the bundle sheath plastids of the 6:30 a.m. samples, while no starch was present in the 8:30 a.m. samples. This suggests that hydrolysis of the stored starch had not been quite completed by 6:30 a.m. but was finished by 8:30 a.m. It is not unreasonable to assume that some photosynthetic activity had occurred prior to 8:30 a.m. Presumably the photosynthetic rate at this time was so low that the rate with which sugar moved into the sheath cells was less than the rate of its passing from the sheath cells into the vascular elements; consequently no starch was deposited and the hydrolysis and translocation of the starch formed the previous day was completed. In the later hours of the day more sugar is manufactured than can be translocated by the vascular bundles, and this excess of sugar is temporarily stored as starch in the bundle sheath plastids. Later, when the cessation or slowing of photosynthesis occurs, this starch is hydrolyzed and translocated into the bundles. This interpretation is consistent with all observed facts and offers a logical explanation for the presence of the specialized plastids of the bundle sheath.

OBSERVATIONS ON OTHER GRASSES

Maize belongs to the subfamily Panicoideae which includes the Andropogoneae, the Maydeae, and the Paniceae. Schwendener (1890) found that the majority of the Panicoideae have a parenchyma sheath but no mestome sheath enclosing the vascular bundles. Sorghum is a member of the Andropogoneae. A study of leaf sections disclosed a situation similar to that in maize. The parenchyma sheath cells have unusually large, pale-green chloroplasts containing many starch grains. The occurrence of a diurnal cycle of starch

deposition and removal probably exists in these plastids as in maize, but this was not established.

The common cereals—oats, wheat, and barley—belong to the subfamily Pooideae. A cursory examination was made of their leaf histology. Our studies were made only on fixed sections of young leaves collected in the afternoon. Possibly different conditions would be found in older leaves, since Percival (1921) states that the outer sheath of older leaves of wheat contains few or no plastids. In these cereals each leaf bundle is surrounded by an inner and outer layer of cells. The parenchyma sheath cells have numerous plastids which, however, are smaller than the plastids of the mesophyll. The mesotome sheath has no plastids. Only small amounts of starch, apparently lying in a central region of the plastid, were found in the parenchyma sheath plastids and also in the mesophyll plastids. The parenchyma and mesophyll plastids of wheat, oats, and barley had so little starch that their leaves gave only a perceptible color with I-KI. On the other hand, the great amount of starch found in the parenchyma sheath plastids of corn and sorghum gives their leaves an intense black color with I-KI. The parenchyma sheath plastids were found concentrated at the side of the cell bordering the mesophyll. The above observations hold for all three genera, but slight differences were noted. The greatest size difference between the sheath plastids and the mesophyll plastids was found in the barley leaf, although a difference in size exists in both wheat and oats (fig. 7). In structure and function, the parenchyma sheath plastids of wheat, oats, and barley, all members of the Pooideae, are obviously different from the bundle sheath plastids of maize and sorghum which belong to the Panicoideae. It will be of interest to ascertain to what extent the members of the two subfamilies of grasses differ in this respect.

SUMMARY

The parenchyma sheath cells enclosing the vascular bundles of the corn leaf contain specialized plastids, green in color, concerned with the elaboration of starch. The starch grains are formed in definite vacuole-like regions in the plastid. A plastid may have as many as 40 starch grains. Starch is deposited in these plastids only when the rate of movement of sugar from the mesophyll cells into the bundle sheath cells is greater than the rate with which sugar passes from the sheath cells into the vascular elements. The bundle sheath plastids deposit starch increasingly during the day. At night this starch is hydrolyzed to soluble carbohydrates and translocated so that the plastids are free of starch by morning. No starch was found in the mesophyll plastids at any time during the day or night. The bundle sheath plastids of sorghum are similar in function to those of maize; this specialization of the bundle sheath plastids may be typical of the subfamily

Panicoideae. The parenchyma sheath plastids of wheat, oats, and barley, all members of the subfamily Pooideae, are different in size and function from those of maize and sorghum.

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THE INHERITANCE OF CERTAIN CHARACTERS IN A CROSS
OF TWO AMERICAN SPECIES OF LACTUCA

THOMAS W. WHITAKER

INTRODUCTION

Two American species of *Lactuca*, *L. canadensis* L. and *L. graminifolia* Michx., are endemic in the eastern portions of the United States and Canada. In general *L. canadensis* ranges from Nova Scotia westward to Saskatchewan and as far south as Georgia, Alabama, Louisiana, and Arkansas and occurs in dry or moist open ground. *Lactuca graminifolia* is found farther south than *L. canadensis*. Its range extends from South Carolina to Florida and west as far as Texas. It usually occurs in rich soil in fields or woods.

Lactuca canadensis and *L. graminifolia* have seventeen pairs of chromosomes (Babcock *et al.* 1937). There is good evidence that the American species of *Lactuca* (with one exception) are amphidiploids, although the exact steps in their origin remain obscure. They are assumed to have originated by hybridization of Old World species of *Lactuca* with eight and nine chromosomes followed by amphidiploidy.

The present study was initiated with the primary purpose of investigating all available species of *Lactuca* as possible sources of desirable genes for introduction into cultivated lettuce, *L. sativa*. The data reported in the present paper have been incidental to our main project, but it is felt that these observations may contribute to a better understanding of the characters which differentiate certain species in nature. In analyzing the relations between these two species (*L. canadensis* and *L. graminifolia*) it may be possible to throw some light on the hypothesized origin of the American species of *Lactuca*.

The relationships between these two species are unique, and differ in detail from other reported cases of this kind (see Goodwin 1938; Winge 1938). First, they are quite distinct entities morphologically, and would be considered "good species" by even the most conservative taxonomist. Second, in reciprocal crosses the F_1 and succeeding generations are extremely fertile. Third, the species under consideration are not ordinary diploids or tetraploids, but euploids of some sort, most probably amphidiploids. Fourth, both species are predominantly self-pollinated and are self-fertile.

As mentioned above, both *Lactuca graminifolia* and *L. canadensis* have seventeen pairs of chromosomes. Usually there is little or no multivalent formation, the entire complement being composed of bivalents at first metaphase. In the F_1 hybrid there is regular pairing of the chromosomes of the

two parental species. An examination of several F_2 plants indicates that meiosis follows a normal course in all of those examined.

DESCRIPTION OF MATERIALS

In 1933 the late J. B. Norton observed in the vicinity of Hartsville, South Carolina, plants which seemed to be intermediate between *Lactuca canadensis* and *L. graminifolia*. These plants were found in locations where the two species were growing together, and were evidently segregates, produced as a result of natural crossing between them.

Norton collected seed of both species, and of the intermediate plants. Starting with seed from this source, the present study has extended over a period of several years. We were able to produce, without difficulty, F_1 hybrids between the two species. The F_1 and plants from subsequent generations proved to be fully as fertile as the parental species. Under our conditions both species have been very uniform. The two species and the F_1 are described below (see figures 1, 2).

Description of *Lactuca canadensis* L. Stems stout, erect, 2–3 m. high, leafy, glabrous, paniculate above; basal leaves sparingly hirsute with scattered long and short hairs on upper surface, and long hairs on midrib both above and below; cauline leaves largely glabrous with few long hairs on midribs; basal leaves spatulate, dentate to pinnatifid; cauline leaves sinuate pinnatifid; involucre 10–12 mm. long; bracts linear-lanceolate to lanceolate; pollen grains yellow; ligules orange yellow; achenes flat, oval, black, narrow-margined, with single prominent rib in the middle of each face, 3–4 mm. long, contracted into slender beaks 1–2 mm. long; biennial, seed planted in the spring makes only rosette of leaves until the following spring when seed stalk develops.

Description of *Lactuca graminifolia* Michx. Stems slender, 0.5–1.0 m. high, glabrous, paniculate above; leaves linear, basal mostly pinnatifid, with a few narrow spreading or deflexed lobes, others entire; involucre 18–20 mm. long; bracts linear-lanceolate to lanceolate; pollen grains grey; ligules purple-blue, achenes flat, oblong-elliptical, dark purple-brown, narrow-margined, with single prominent rib in the middle of each face, 5–6 mm. long, contracted into slender beaks 3–4 mm. long; in South Carolina, according to Norton, normally a winter annual blooming early in the spring from autumn sown seed; in coastal Southern California it grows well as either a winter or a summer annual.

Reciprocal cross pollinations between *Lactuca canadensis* and *L. graminifolia* during three seasons have invariably produced an abundance of viable

Explanation of figures 1–3

FIG. 1. Left to right: F_1 , *Lactuca canadensis*, *L. graminifolia*. FIG. 2. F_2 segregates from the cross *Lactuca canadensis* \times *L. graminifolia*. FIG. 3. F_2 individuals showing segregation for growth habit. Annuals for the most part in flower. Low plants in foreground are biennials; no indication of seed stalk formation.



crossed seed. Each species appears to produce seed fully as abundantly when pollinated by the other species as when self-pollinated.

Description of F_1 (*Lactuca canadensis* \times *graminifolia*). The F_1 plants are approximately intermediate (fig. 1) between the two species in most respects, including height, size and shape of rosette leaves, color and shape of ligules, color and size of achenes. In our work the annual habit proved to be dominant over biennial habit; grey color of pollen grains dominant over yellow color. Lobing of the cauline leaves was dominant over entire leaves, although they were not nearly as pinnatifid as *L. canadensis* (fig. 4). Table 1 lists the prominent contrasting characters of the two species, and indicates the appearance of these characters in the F_1 .

TABLE 1. *Table of prominent contrasting characters.*

	<i>L. canadensis</i>	<i>L. graminifolia</i>	F_1
Growth habit	biennial	annual	annual
Ligules	orange yellow	purple blue	purple
Pollen	orange	grey	grey
Involucral bracts			
(length)	13-14 mm.	19-20 mm.	18-19 mm.
Cauline leaves	lobed, pinnatifid	entire, lanceolate	lobed
Height	2-3 m.	0.5-1.0 m.	1.2-2.5 m.

EXPERIMENTAL RESULTS

A. Inheritance of Pollen Grain Color. As noted above, *Lactuca canadensis* produces pollen grains with a deep orange color; *L. graminifolia* has grey pollen grains. The F_1 plants have grey pollen grains, indicating that the gene for grey color of pollen grains is dominant over that for orange color. This gene segregates very sharply in the F_2 with no suggestion of intermediate colors. In this case pollen color acts as an ordinary sporophytic character, since there is no segregation for color in the F_1 plants. It seems likely that the substances responsible for color are produced by the sporophyte.

From F_1 plants grown in 1937 three F_2 families were obtained. A total of 635 individuals were scored for pollen color in the F_2 ; the results are recorded in table 2. Of ten F_3 families, four were segregated and six appeared to be homozygous (table 3). It is clearly evident from the data of tables 2 and 3 that a single gene is responsible for pollen grain color.

B. Inheritance of Plant Growth Habit. The inheritance of growth habit has been investigated in several species of plants belonging to widely separated families. With one exception the annual habit has been shown to be dominant over the biennial habit (Clarke 1935; Abegg 1936), and in all cases it was governed by a single gene difference. Melchers (1937) reports that growth habit in *Hyoscyamus niger* is controlled by a single gene; in this species the annual habit is recessive to the biennial.

As noted in a previous report (Thompson *et al.* 1941), the annual habit is dominant over the biennial in several interspecific crosses of *Lactuca*. A

TABLE 2. Segregation for pollen color in F_2 families.

Family No.	No. of plants	Pollen color				χ^2
		Orange	Grey	Expected orange	Expected grey	
13454	554	137	417	138.5	415.5	0.04
33111-1 ..	38	9	29	9.5	28.5	0.017
33112-1 .	43	16	27	10.7	32.1	3.42
Total .	635	162	473	(df = 3, P = 0.4)		3.477

limited number of observations have been made on the inheritance of annual vs. perennial growth habit. In nature *Lactuca graminifolia* is an annual and *L. canadensis* is biennial. To determine the quantitative expression of this character, seed of the parental species, the F_1 , and one family of F_2

TABLE 3. Segregation for pollen color in F_3 families.

Family No.	Phenotype of F_1 parent	No. of plants	Pollen color		χ^2
			Orange	Grey	
30001	grey	10		10	
30003	orange	19	19		
30004 ...	grey	17		17	
30005	grey	5	1	4	0.06
30008	grey	24	5	19	0.22
30009	orange	15	15		
30010	orange	10	10		
30011	grey	72	24	48	1.18
30012	grey	70	47	23	2.30
30013	orange	3	3		

plants were planted during the early part of August. After four weeks in the seed bed the plants were transplanted to the field and were scored for growth habit from October through November. At this time (11/10/39) our records show that all plants of *L. graminifolia* and the F_1 hybrids were in full flower. Plants of *L. canadensis* did not produce seed stalks until the

TABLE 4. Segregation of annual vs. biennial habit of growth in F_2 and F_3 families.

Family No.	Phenotype of parent	Total No. of plants	Annual	Biennial	χ^2
13454 (F_2)	annual	334	257	77	0.67
33111-1-16 (F_3)	"	7	6	1	
33111-1-18 (F_3)	"	16	12	4	
30004 (F_3)	biennial	23	0	23	
30005 (F_3)	annual	10	4	6	
33111-1-33 (F_3)	"	10	10		
30008 (F_3)	"	17	10	7	
33112-1-33 (F_3)	biennial	10	0	10	

following March. Table 4 shows the segregation in the F_2 family and a few of the F_3 observations (fig. 3). These rather meager observations, while not conclusive, seem to indicate that growth habit is probably dependent upon a single gene difference.

C. Inheritance of Leaf Lobing. The basal or rosette leaves of *Lactuca graminifolia* are linear and pinnatifid, usually with several narrow lobes either spreading or deflexed; in contrast the cauline leaves are linear-lanceolate and entire. On *L. canadensis* the rosette and flower-stalk leaves are of the same general character, spatulate and dentate to sinuate pinnatifid. In the F_1 , leaf shape is approximately intermediate between the two parental species, but both rosette and cauline leaves are distinctly pinnatifid (fig. 4). In the F_2 , most plants have rosette leaves which are more or less pinnatifid. In some cases only one leaf of the rosette will be lobed. With regard to the cauline leaves there is segregation into two types, lobed or

TABLE 5. Segregation for lobing in F_2 .

Family No.	Phenotype of parent	Total No. of plants	Lobed	Entire	χ^2
13454	lobed	746	582	164	3.62

pinnatifid and entire (fig. 5). Records from one F_2 family of 746 individuals are summarized in table 5. Of ten F_3 families, four appeared to be homozygous and six were segregating. However, the number of plants scored from each family was not sufficient to make this determination accurate, but there is strong evidence from the one F_2 family of 746 individuals that the basic leaf pattern is controlled by a single gene.

Although the basic pattern of the leaf (lobed vs. entire) seems to be governed by a single gene, there is apparently a group of modifiers at work which are responsible for the number and shape of the lobes. No attempt has been made to analyze these factors.

DISCUSSION

The characters selected for study all are apparently simple Mendelian gene differences. However, there are a number of other segregating char-

Explanation of figures 4-6

FIG. 4. Cauline leaves—two leaves from each plant, dorsal and surface view; left to right: *Lactuca graminifolia*, entire; F_1 (*L. graminifolia* \times *L. canadensis*), lobed; *L. canadensis*, lobed. FIG. 5. Cauline leaves—entire leaves from three F_2 segregates (dorsal and surface view of leaves from each plant). FIG. 6. Cauline leaves—lobed leaves from three F_2 segregates (dorsal and surface view of leaves from each plant). Note the variation in the pattern of lobing, from the minimum condition on the left to the highly pinnatifid condition of the center leaves.



acters which appear to have a more complex basis. With respect to ligule color, F_2 individuals range from those with a light orange color quite similar to *Lactuca canadensis* to individuals almost lacking in color or with only a faint tinge of purple.

If these two species are amphidiploids, the fact that bivalents are formed regularly at first meiotic metaphase indicates that they were derived from hybridization between rather distantly related species (Poole 1932; Huxley 1943). On this basis segregation for at least some of the character differences between the two amphidiploids should follow along simple lines, and this has been supported by actual observations. This evidence when combined with the work of Thompson (1942), who has actually synthesized an amphidiploid *Lactuca* by crossing a seventeen-chromosome species with a nine-chromosome one, lends indirect support to the original postulate of Babcock, Stebbins and Jenkins (1937) that the seventeen-chromosome species of *Lactuca* are amphidiploids obtained from a cross (or several crosses) between a nine-chromosome and an eight-chromosome species followed by doubling.

From the evidence produced in this investigation it is clear that the conspicuous differences between these two species are for the most part simple gene differences, probably on the same level as those which distinguish many varieties of cultivated plants. It is also probable that these two species are very closely related, having diverged from a common amphidiploid ancestor. The fact that the species are able to maintain themselves as distinct entities in nature is certainly not related to the lack of fertility of the hybrids, since all of the individuals resulting from the cross are fully as fertile as either species. It seems more likely that lack of success of the hybrids in nature can be attributed to their inability to encounter an ecological niche to which they are well adapted. One further fact seems important in this connection. I am told by Dr. R. C. Thompson that in nature *L. graminifolia* flowers well in advance of *L. canadensis*, and ordinarily has completed the flowering cycle before the flowers of *L. canadensis* begin to open. This differential timing of the reproductive cycle probably accounts for the fact that there is very little hybridization of these two species even though there is a decided overlapping of their respective ranges.

SUMMARY

1. Two species of *Lactuca*, *L. graminifolia* and *L. canadensis*, have been successfully hybridized. The F_1 progeny and plants of subsequent generations are as fertile as either parent.

2. A genetic analysis of three marked differences between these two species has shown that pollen color (grey vs. orange), leaf lobing (lobed vs. entire), and growth habit (annual vs. biennial) are each dependent upon single-gene differences.

3. The evidence accumulated in this work seems to indicate that the differences between these two very distinct species are for the most part dependent upon simple gene differences.

4. The relation of the observations reported in this paper to the theory of the amphidiploid origin of the seventeen-chromosome *Lactucas* is discussed.

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CYTOGENETIC STUDIES OF HYBRIDS WITH
"MAKHA" WHEATT. C. CHIN AND C. S. CHWANG¹

INTRODUCTION

On the basis of their chromosome numbers, the wheats fall into three groups: the so-called diploid wheats with $n = 7$, the tetraploids with $n = 14$, and the hexaploids with $n = 21$. These groups are taxonomically, as well as cytologically, distinct. Within each group the various species, with the notable exception of *Triticum timopheevi* of the tetraploid group, have homologous chromosomes which pair normally in hybrids. Crosses between groups show that the 21 different chromosomes of the hexaploids are composed of three sets (genoms) of seven, which are commonly designated A, B, and C, respectively, while the chromosomes of the tetraploids consist of sets A and B, and those of the diploids of set A. *Triticum timopheevi* is designated AAGG by Lilienfeld and Kihara (1934) and Kihara (1937), and AA $\beta\beta$ by Kostoff (1936).

Although the designation of the various sets of chromosomes by letter is a convenient shorthand device, it does not give an entirely accurate picture, particularly as regards the A set. As Kihara (1937) has pointed out, the A genom of the diploid wheats is not truly homologous with the A of the tetraploids, although the two sets are capable of forming up to seven pairs in hybrids. Even in hexaploid \times tetraploid hybrids, where the respective A and B sets ordinarily show normal pairing, multivalent configurations and other irregularities are found when certain varieties are used (Love 1941; Chin & Chwang 1942). That there are intergenomic and possibly intragenomic homologies is shown by the fact that one or more pairs may be formed in haploids of wheats of the hexaploid and tetraploid groups. This conclusion is borne out by the occurrence of trivalents in tetraploid \times diploid hybrids (Kihara & Nishiyama 1928; Aase 1930) and of various multivalents in hexaploid \times tetraploid hybrids. These multiple configurations are presumably due to autosyndesis conditioned by structural changes between non-homologous chromosomes (Darlington 1937; Love 1941; Chin 1942; Chin and Chwang 1942).

¹ This paper was transmitted to the editor by Dr. Barbara McClintock, to whom it was sent by T. C. Chin. In preparing it for publication, the editor had the generous cooperation of Dr. E. R. Sears. Because of current conditions, it was necessary to dispense with the usual intercourse between authors, reviewer, and editor; the authors could not be consulted about some of the modifications made by Dr. Sears, nor had they an opportunity of seeing the paper in proof. To publish the numerous tables recourse was had to the Lucien M. Underwood Memorial Fund.

Triticum macha Dekapr. & Menab. is a new species of wheat of the hexaploid or *vulgare* group found in West Georgia (Dekaprelevitch & Menabde 1932). Its discoverers regarded it as a possible ancestor of the present-day *T. spelta*, which it resembles in the toughness of its glumes. It is distinct from *T. spelta*, however, in the method of disarticulation of the rachis (Hector 1936), *T. spelta* fracturing below the point of attachment of the spikelets and *T. macha* above. As far as the present authors are aware, cytogenetic evidence of its relationship with other wheats is as yet lacking. This paper is a preliminary report of a series of cytogenetic investigations of hybrids between "Makha" and other wheats, with special emphasis on possible phylogenetic relationships.

MATERIAL AND METHODS

Triticum macha was obtained from the Kansas State Agricultural College, Manhattan, Kansas. It was crossed with the two hexaploid species *T. vulgare* and *T. spelta*, and with the three tetraploid species *T. durum*, *T. turgidum*, and *T. dicoccoides* in the summer of 1941. Both *T. vulgare* and *T. spelta* were beardless, while *T. turgidum*, *T. durum* var. *leucurum* Körn., and *T. dicoccoides* var. *Aaronsohni* were all fully bearded. *T. macha* has short awns. Spikes and spikelets of most of the species used are shown in figures 1 and 3.

The cytological studies were made from aceto-carminic smears prepared in the summer of 1942 at Chengtu. The majority of the slides were mounted in Zirkle's fluid, and the rest in Canada balsam. The drawings were made with the aid of a camera lucida.

GENETICAL OBSERVATIONS

Hexaploid Hybrids. 1. *T. vulgare* \times *T. macha*. Only two hybrid plants were obtained—one from each of the two *vulgare* varieties used. Both plants showed signs of chlorophyll deficiency and were very weak and completely sterile. No pollen mother cells could be found. The spikes (fig. 2, no. 2; fig. 3, no. 7) were beardless, as in the *vulgare* parents, whereas the rachis was fragile, as in *T. macha*. Thus fragility of rachis and beardlessness were apparently completely dominant.

2. *T. spelta* \times *T. macha*. The F_1 plants of this cross (fig. 2, no. 1; fig. 3, no. 6) were also very weak and showed signs of chlorophyll deficiency, but they reached maturity. The amount of sterility was 63.5 per cent. The seedlings were prostrate, as were those of both parents. The spike was of intermediate density and was beardless like *T. spelta*. The rachis was fragile both above and below the spikelets, showing that both types of disarticulation tend to be dominant, and suggesting that two independent genes are involved. The shoulder of the outer glume was narrow, as in *T. macha*.

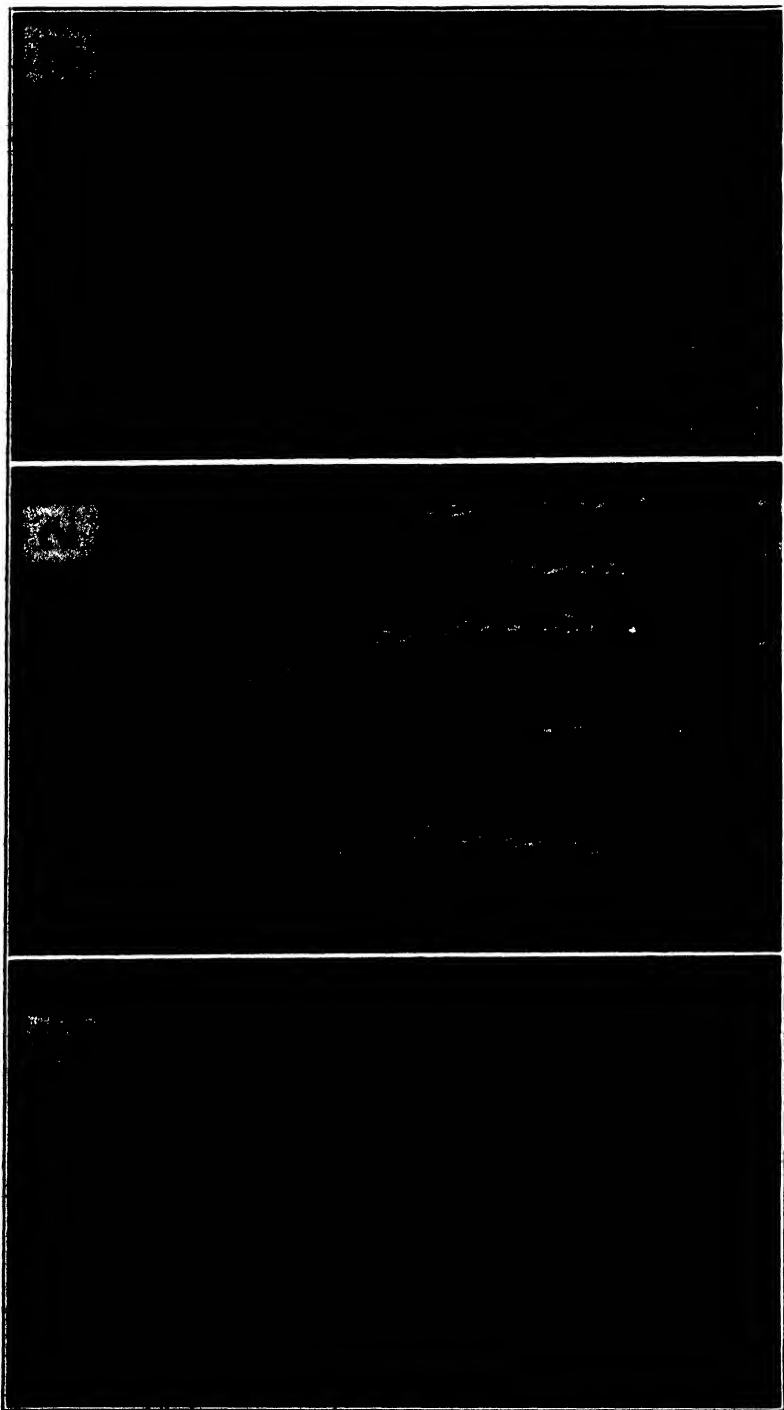


FIG. 1. Spikes of (1) *T. spelta*, (2) *T. macha*, (3) *T. dicoccoides*, (4) *T. turgidum*, and (5) *T. durum*. $\times 0.2$. FIG. 2. Spikes of (1) *T. spelta* $\times T. macha$, (2) *T. vulgare* $\times T. macha$, (3) *T. macha* $\times T. dicoccoides$, (4) *T. macha* $\times T. turgidum$, and (5) *T. macha* $\times T. durum$ $\times 0.2$. FIG. 3. Spikelets of (1) *T. spelta*, (2) *T. macha*, (3) *T. dicoccoides*, (4) *T. turgidum*, (5) *T. durum*, (6) *T. spelta* $\times T. macha$, (7) *T. vulgare* $\times T. macha$, (8) *T. macha* $\times T. dicoccoides$, (9) *T. macha* $\times T. turgidum$, and (10) *T. macha* $\times T. durum$. $\times 0.2$.

Pentaploid Hybrids. All three of these hybrids (fig. 2, nos. 3-5; fig. 3, nos. 8-10) had awns of intermediate length and spikes much longer than those of either parent. The degree of sterility was 37.4 per cent in *T. macha* \times *T. turgidum*, 40.5 per cent in *T. macha* \times *T. durum*, and nearly 100 per cent in *T. macha* \times *T. dicoccoides*. Most of the F_1 plants of the last combination were completely sterile.

CYTOLOGICAL OBSERVATIONS

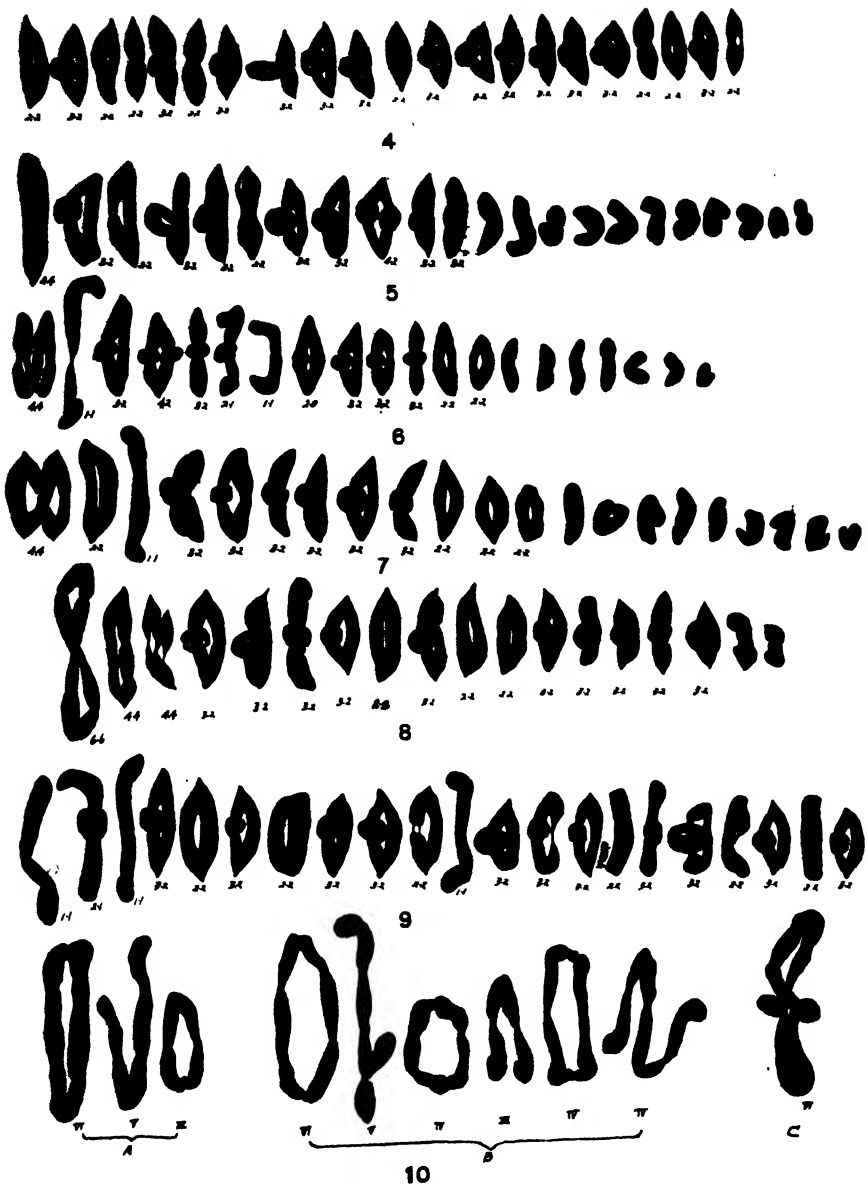
Hexaploid Hybrid. Associations of from one to six chromosomes were observed at first meiotic metaphase in *T. spelta* \times *T. macha* (table 1). The

TABLE 1. *Combinations of configurations observed in Triticum spelta* \times *T. macha*.

Number of microsporocytes	Configurations					
	I	II	III	IV	V	VI
1	2	13	.	2	..	1
1	2	15	.	1	..	1
2	2	17	1
1	1	18	.	.	1	.
1	3	17	.	.	1	.
1	5	16	.	..	1	..
1	2	16	1	.	1	.
1	.	15	.	3	.	.
3	.	17	.	2
1	2	16	.	2	.	.
2	1	17	1	1	.	..
2	.	18	2	.	.	.
3	2	17	2	.	.	.
5	.	19	.	1	.	.
6	2	18	.	1	.	.
7	1	19	1
1	3	18	1	.	.	.
29	.	21
3	2	20
3	4	19
74	0.93	19.08	0.28	0.36	0.05	0.05

average number of chromosomes involved in multiple configurations was 2.90, and the maximum number was 14—in one association of six and two associations of four (fig. 8). The maximum number of associations of four in the same cell was three. Of 74 cells, 39 (52.7 per cent) had multiple configurations; and 20 of these 39 had more than one multiple configuration. Twenty-nine of the 74 cells had 21 bivalents, as in figure 9.

The pairing intensity in the hybrid, as measured by the number of half-chiasmata per metaphase chromosome, was somewhat lower than in *T. macha* itself (fig. 4)—2.16 compared with 2.45. Even the bivalents considered by themselves had only 2.30 half-chiasmata per chromosome in the hybrid. Table 2 summarizes the data on the number of chiasmata in the various types of configurations.



FIGS. 4-9. First meiotic metaphase configurations in (4) *Triticum macha*, (8, 9) *T. spelta* × *T. macha*, (5) *T. macha* × *T. turgidum*, (6) *T. macha* × *T. durum*, and (7) *T. macha* × *T. dicoccoides*. Each figure shows the chromosomes from a single microsporocyte. The two numbers accompanying each bivalent and multivalent indicate the number of chiasmata (left) and the number of chromosomes (right) involved in that configuration. × 730. FIG. 10. Multivalent configurations in (A) *T. macha* × *T. turgidum*, (B) *T. macha* × *T. durum*, and (C) *T. spelta* × *T. macha*. × 730.

Terminal chiasmata constituted 82.8 per cent of the total in *T. spelta* × *T. macha*. The number of interstitial chiasmata was more variable from cell to cell than was the number of terminal chiasmata. This may be attributed to the tendency for terminal affinity to cause the localization of metaphase chiasmata in the terminal position (Darlington 1937). Also, a possible source of variation in the number of interstitial chiasmata lies in the structural changes of certain chromosomes, these changes presumably being capable of preventing the terminalization of certain chiasmata.

TABLE 2. *Frequencies of configurations with various numbers of chiasmata. Values are given in percentages of the total number of chromosomes observed of each hybrid.*

6x				5x		
Hybrids:		<i>T. spelta</i> × <i>T. macha</i>	<i>T. macha</i> × <i>T. turgidum</i>	<i>T. macha</i> × <i>T. durum</i>	<i>T. macha</i> × <i>T. dicoccoides</i>	
Types of configuration and number of chiasmata	I	0	3.5	21.7	21.6	20.8
	II	1	9.2	4.3	8.0	4.2
		2	41.9	21.4	30.8	27.5
		3	33.2	40.6	30.6	33.8
		4	0.9	1.1	2.9	...
	III	2	3.1	1.7	3.0	0.8
	IV	3	1.9	4.0	1.7	3.1
		4	3.2	2.9	0.6	8.3
		5		0.6		
	V	4	1.2			
	VI	6	1.4		0.9	1.6
		7		1.7
		8	0.5	
	No. cells observed		30	20	20	11

A correlation of -0.151 was found between the number of chiasmata per cell and the number of univalents. This value is statistically insignificant, suggesting that failure of pairing between one homologous pair of chromosomes may result in an increase in the number of chiasmata in some other pairs (Ribbands 1937).

The association of six was always in the form of a ring (figs. 8, 10 C), while the associations of five and of three were always chains.

Chromosome bridges were observed in 13.8 per cent of the microspores at first anaphase (table 3). These bridges presumably resulted from crossing-over within inverted or duplicated segments, although few were accompanied by fragments. The bridges appeared to involve the long arm of chromosomes with subterminal centromeres (fig. 16).

No basis was found in the cytological data for the high degree of sterility (63.5 per cent) of this hybrid. Examination of pollen grains showed only 17.8 per cent aborted grains.

Pentaploid Hybrids. The pentaploid hybrids also had associations of from one to six chromosomes (table 4; figs. 5-7, 10 A, B). In the average number per cell of the various configurations, these hybrids were very similar to certain of those reported by Love (1941) between varieties of *T. vulgare* and varieties of *T. dicoccum* and *T. durum*—notably the crosses involving the *durum* variety Pentad. For *T. vulgare* var. McMurachy \times *T. durum* var. Pentad, he found almost exactly the same average numbers of the various configurations as the combined average for the three hybrids reported here.

TABLE 3. *Frequency of bridges at first and second anaphase.*

Hybrid	Stage of meiosis	No. bridges observed	No. cells examined	Per cent with bridges
<i>T. spelta</i> \times <i>T. macha</i>	Anaphase I	12	87	13.8
	Anaphase II	0	Many	0.0
<i>T. macha</i> \times <i>T. turgidum</i>	Anaphase I	10	265	3.8
	Anaphase II	26	178	14.6
<i>T. macha</i> \times <i>T. durum</i>	Anaphase I	4	240	1.7
	Anaphase II	42	274	15.4
<i>T. macha</i> \times <i>T. dicoccoides</i>	Anaphase I	2	37	5.4
	Anaphase II	2	10	20.0

The fact that several microsporocytes had as few as four or five univalents suggests that there was some pairing among chromosomes of the C genom of *T. macha*.

Apparently the hexaploid hybrid involving *T. macha* had the capacity for forming one more association of four than had the pentaploid hybrids. This is indicated by the fact that one association of six and one of four, or two associations of four, were the maximum amount of multivalent formation in the pentaploids; whereas one association of six and two of four, as well as three associations of four, were found in the hexaploids. It is not clear whether the additional association of four in the hexaploid was composed entirely of chromosomes from the C genom, or whether it was composed partly of chromosomes from the C genom and partly of chromosomes from the A or B genom.

As in the hexaploid hybrid, the association of six was always in the form of a ring, and the associations of five and three were always chains.

The number of half-chiasmata per chromosome, when calculated on the basis of 14 possible pairs (that is, 28 chromosomes per cell), was 2.41 for *T. macha* \times *T. turgidum*, 2.29 for *T. macha* \times *T. durum*, and 2.33 for *T.*

macha \times *T. dicoccoides*. These figures are to be compared with 2.45 for *T. macha* itself and 2.16 for *T. spelta* \times *T. macha*. It thus appears that the pairing intensity is more nearly normal in the pentaploids than in the hexaploid hybrid. In fact, when calculations are made for only the bivalents actually present, the values become 2.57, 2.39, and 2.45, respectively, for the three pentaploid hybrids—approximately the same as for *T. macha* itself. As in

TABLE 4. *Combinations of configurations observed in pentaploid hybrids.*

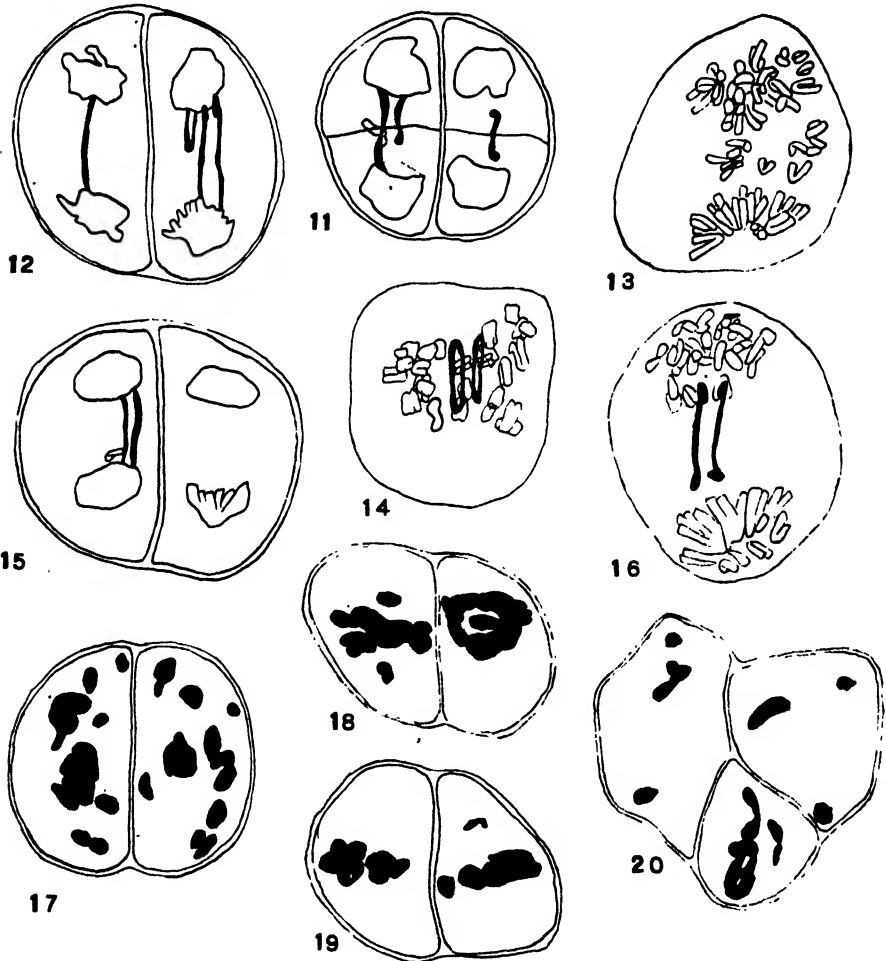
Number of microsporocytes in			Configurations					
<i>T. macha</i> \times <i>T. turgidum</i>	<i>T. macha</i> \times <i>T. durum</i>	<i>T. macha</i> \times <i>T. dicoccoides</i>	I	II	III	IV	V	VI
		1	5	10	..	1	..	1
1	1	..	7	11	1
1	9	10	1
1	7	10	1	..	1	..
..	1	..	9	8	2	1
		1	7	10	..	2
2	..	1	9	9	..	2
	1	..	4	12	1	1
		1	6	11	1	1
1	5	12	2
		1	5	13	..	1
4	1	2	7	12	..	1
2	1	2	9	11	..	1
1	11	10	..	1
1	4	14	1
	2	..	6	13	1
1	1	..	8	12	1
	1	..	10	11	1
4	7	1	7	14
1	4	1	9	13
20		..	7.60	11.80	0.25	0.55	0.05	0.10
	20	..	7.55	12.65	0.35	0.20	0.00	0.05
		11	7.27	11.45	0.09	1.00	0.00	0.09
Combined total: 51			7.51	12.06	0.25	0.51	0.02	0.08

the hexaploid hybrid, the chiasmata were mostly terminal—77.3 per cent terminal in *T. macha* \times *T. turgidum*, 81.4 per cent in *T. macha* \times *T. durum*, and 81.3 per cent in *T. macha* \times *T. dicoccoides*. Interstitial chiasmata were again more variable in number than were terminal chiasmata.

In the pentaploids the number of univalents was negatively correlated with the number of chiasmata, values of -0.674 and -0.629 being obtained for *T. macha* \times *T. turgidum* and *T. macha* \times *T. durum*, respectively. These values are beyond the one per cent point of significance.

In the frequency of anaphase bridges the pentaploid hybrids differed strikingly from the hexaploids, in that bridges were much more frequent at second than at first anaphase (table 3). The three pentaploids averaged about five times as many microsporocytes with bridges at second as at first ana-

phase. This high frequency of second anaphase bridges appears not to be explainable on the basis of inversions. Whatever the cause of the bridges may have been, they apparently involved at least three different chromosomes in *T. macha* \times *T. durum* (fig. 12) and at least two in *T. macha* \times *T. turgidum* and *T. macha* \times *T. dicoccoides* (figs. 11, 15). The bridges appeared to be confined to the long arm of chromosomes with subterminal centromeres, except in *T. macha* \times *T. durum*, where chromosomes with submedian and median centromeres seemed to be involved also.



FIGS. 11, 12, 15. Bridges at second anaphase in (11) *T. macha* \times *T. turgidum*, (12) *T. macha* \times *T. durum*, and (15) *T. macha* \times *T. dicoccoides*. $\times 500$. FIG. 13. Normal anaphase I in *T. macha* \times *T. dicoccoides*. $\times 500$. FIG. 14. Multiple configurations delayed in division in *T. macha* \times *T. durum*. $\times 500$. FIG. 16. Two single bridges at first anaphase in *T. spelta* \times *T. macha*. $\times 500$. FIGS. 17-20. Crumbled chromosomes in *T. macha* \times *T. dicoccoides*. $\times 500$.

Long chains of three sometimes failed to congress in the pentaploids. The multiple configurations usually separated more slowly than the normal bivalents (fig. 14).

In *T. macha* \times *T. dicoccoides* the first division was normal (fig. 13), but the chromosomes usually crumbled into masses at the second division (figs. 17–20). The abnormality occurred either before or after the formation of a metaphase plate. The chromatin masses formed varied considerably in number, size, and shape. This crumbling of chromosomes presumably accounts for the high percentage of sterility in this hybrid.

DISCUSSION

Little support is provided by the present investigation for the suggestion of Dekapreleritch and Menabde (1932) that *Triticum spelta* may have been derived from *T. macha*. The irregular meiotic behavior and the low fertility of the *T. spelta* \times *T. macha* F_1 certainly do not favor such a hypothesis; and neither does the fact that the spike of *T. macha* has a type of disarticulation not found in any variety of *T. spelta*.

The exact phylogenetic relationship of *T. macha* to the other species of hexaploid wheat is not at all clear. The fact that the intensity of pairing, as measured by the number of chiasmata, is essentially the same in the pentaploid hybrids as in *T. macha* itself suggests that the A and B genomes of *T. macha* may be identical with those of the emmers except for at least three reciprocal translocations (to account for the ring of six and association of four sometimes found in a single cell). This possibility of close relationship is favored by the relatively high fertility of two of the pentaploid hybrids—about 60 per cent, which is greater than ordinarily found in hybrids between *T. vulgare* and *T. durum* or *T. dicoccum* (Love 1941). Also, the meiotic irregularities of the pentaploid hybrids involving *T. macha* are no greater than in certain of Love's hybrids of *T. vulgare* with *T. durum*.

The possibility that *T. macha* may possess a somewhat different C genom than the other hexaploid wheats arises from the finding that pairing is relatively poorer in *T. spelta* \times *T. macha* than in *T. macha* \times the tetraploid wheats. Furthermore, the method of disarticulation of the spike is fundamentally different in *T. macha* from that in *T. spelta* or *T. vulgare*, and the type of awn is different from that in *T. spelta* and from the various types described by Watkins and Ellerton (1940) for *T. vulgare*. A simple explanation for these differences would lie in the independent origin of *T. macha* as an amphidiploid resulting from a cross of one of the emmers with a species of *Aegilops* having short awns (or lacking awns altogether) and a rachis fragile above the point of attachment of the spikelet.

SUMMARY

Hybrids with *Triticum spelta* and *T. vulgare* show that *T. macha* differs genetically and cytologically from the other hexaploid wheats. It has a dif-

ferent kind of awn and a different type of disarticulation of the rachis. The F_1 plants are very weak and are either completely sterile (*T. vulgare* \times *T. macha*) or about 60 per cent sterile (*T. spelta* \times *T. macha*). At meiosis *T. spelta* \times *T. macha* showed an average of 2.90 chromosomes involved in multivalent configurations and 0.93 in univalents. Bivalents are of reduced chiasma frequency, and bridges are frequent at first anaphase.

Hybrids of *T. macha* with the tetraploid species *T. turgidum*, *T. durum*, and *T. dicoccoides* do not differ greatly from the similar hybrids involving *T. vulgare* or *T. spelta*. Multivalent associations occur, but bivalents are of approximately normal chiasma frequency. Anaphase bridges are found, particularly at the second division. Fertility is high (about 60 per cent) except in *T. macha* \times *T. dicoccoides*, which is almost completely sterile, apparently through crumbling of the chromosomes at the second division. Awns are of intermediate length in these hybrids, and spikes are longer than in either parent.

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HETEROKARYOSIS IN *PENICILLIUM NOTATUM*

GLADYS E. BAKER

It has been recognized through experience that single-spore transfers of *Penicillium notatum* Westling are undesirable in maintaining an active penicillin-producing strain, for this practice is said to result in a less productive strain (Clutterbuck et al. 1932; Foster et al. 1943). Since the single-spore method is commonly regarded as means of securing pure lines in many fungi, it seemed important to investigate the nuclear behavior of this species to see if that might explain the necessity of mass spore transfers.

A penicillin-producing strain of this fungus (N.R.R.L. 1209) was used. Films of modified Czapek-Dox agar were spread on sterile slides and when dry were sown with a water suspension of spores from a seven-day culture on the same agar. The slides were incubated in sterile moist chambers at 25° C. Material was killed and fixed on the slides at intervals of 6, 12, 24, 36, 48, and 72 hours. Of the various fixatives employed, Bouin's and a modified F. A. A. gave the best results. Conidiophores with conidia frequently appeared as early as the 24-hour stage and 48 hours provided a full range of mycelial and conidial development. For nuclear stages of the conidia the spore suspension was put directly on slides with Mayer's adhesive, dried down lightly and immediately killed and fixed. In addition small portions of colonies on agar plates were cut out and fixed. These were embedded in paraffin and sections cut 7 μ and 10 μ thick. All slides were stained in Heidenhain's iron-alum-haematoxylin and counterstained with 1 per cent alcoholic phloxine. These agar-film slides were also used for microchemical tests. For direct observation of germination stages agar slide cultures were prepared after the method recommended by Henrici (1930).

The conidia of *P. notatum* are subglobose, smooth and of varying diameters. Before germination they range from 2.0-4.0 μ in diameter. Microchemically the wall substances give a positive reaction for cutin and pectin, but not for cellulose; for storage substances they give positive tests for glycogen, fats, and proteins. Their enlargement prior to germination is conspicuous, often doubling their size. Conidia produced in the same chain frequently do not separate before they germinate. The wall between two such contiguous cells is conspicuously thinner. A germ tube may be produced from each of these conidia independently, or less commonly from only one of the spores, in which case the nucleus of the second spore may migrate into it (fig. 2).

A conidium typically contains one nucleus and germinates by a single germ tube, or less frequently by two germ tubes (figs. 1, 3). The nucleus

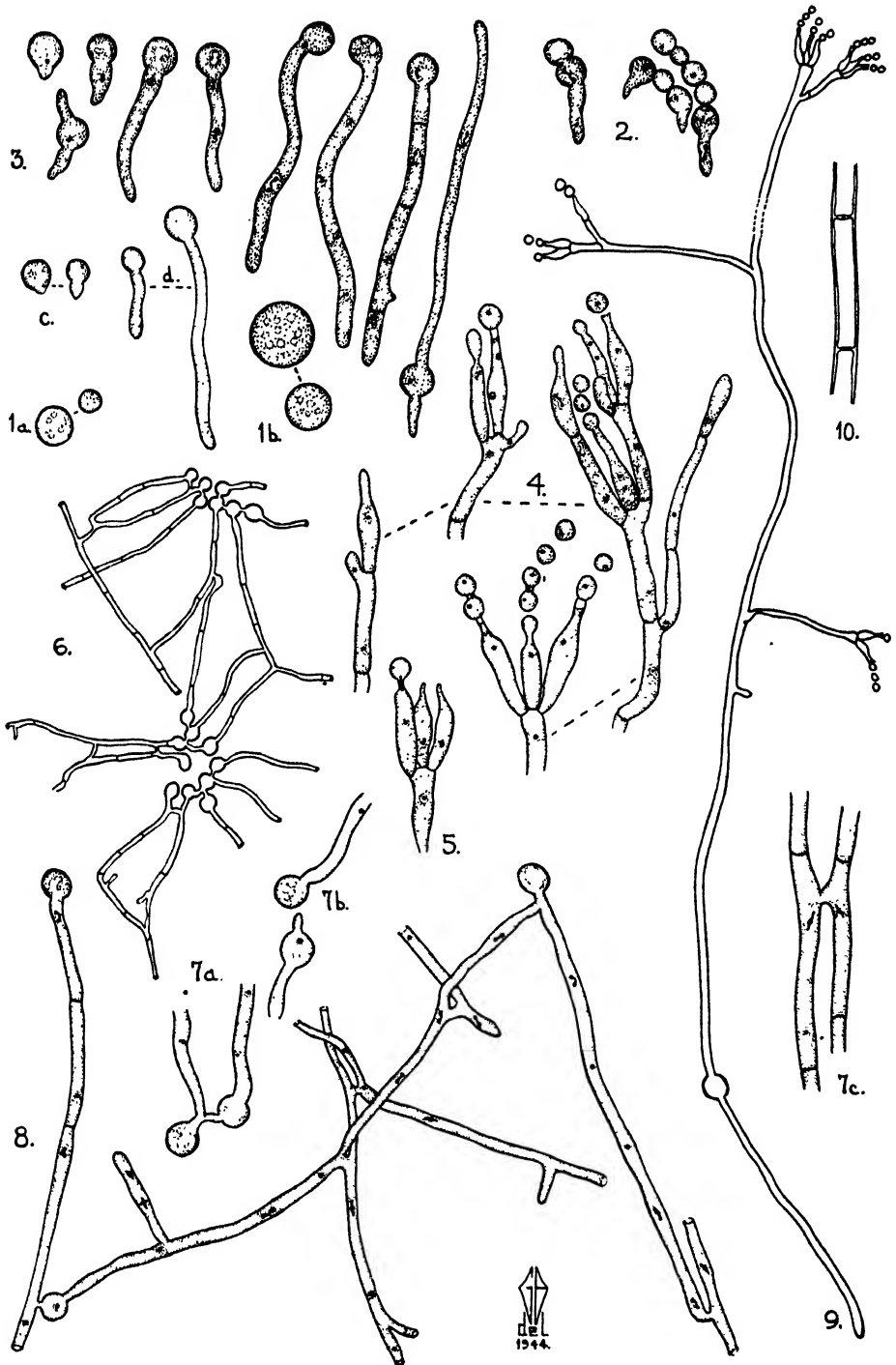
divides as the germ tube is produced. One of the two daughter nuclei may remain in the conidium or near it, the second one moving out into the hypha for further division. Or both the daughter nuclei may move out into the elongating hypha and divide again. Germination of the spores occurs in 6–7 hours after sowing and in two more hours the hypha may be $50\ \mu$ long and in the 4-nucleate stage (fig. 1, *c*, *d*). Occasionally one finds two nuclei in a conidium but they often evince signs of recent division, which suggests that the binucleate condition arose subsequent to separation from the conidiophore. No conidia were found with more than two nuclei. Many nuclear divisions accompany the elongating hyphae. Cross walls may or may not follow these early mitotic divisions. As the hyphae elongate the more distal portions are clearly septate. In the basal portions (nearer the original spore) the nuclei may never become separated by walls, but they are spaced well apart. The mycelial cells are consistently uninucleate in the distal septate regions; elsewhere they may be binucleate or even plurinucleate through intercalary division and lack of immediate septation.

Conidiophores are produced early and freely by the mycelium. The phialides are uninucleate with regular nuclear divisions which provide daughter nuclei for the developing conidia. The first conidium of a series is formed at the apex of the phialide as a swollen vesicular expansion, the connection between it and the phialide gradually contracting so that only a narrow connective remains at maturity, through which the nucleus passes in an attenuated fashion. Once within the spore the nucleus again becomes globose (fig. 5). Successive conidia seem to be formed by continued enlargement and constriction of the phialide behind the first-formed conidium. The process is accompanied by continued mitotic division of the producing phialide.

There is nothing unusual about this behavior. However, in watching the progress of germination one finds that after 12 hours or so the frequency of anastomoses involving the spores and their germ tubes is very striking. Such anastomoses are not unnoted for the *Penicillia* but in connection with their nuclear history may be important. Anastomoses occur between spores by short hyphal connectives, between spores and hyphae, and between ma-

Explanation of figures 1–10

FIG. 1*a*. Spores before germination. $\times 1850$. *b*. Spores at germination. $\times 1850$. *c*. Spores at seven-hour germination stage. $\times 590$. *d*. Spores and hyphae at nine-hour stage. $\times 590$. FIG. 2. Contiguous conidia germinating. $\times 1850$. FIG. 3. Germination stages showing nuclei. $\times 1850$. FIG. 4. Stages in conidiophore and conidia formation. $\times 1850$. FIG. 5. Nucleus passing into first conidium. $\times 1850$. FIG. 6. Germinating and anastomosing spores at 12 hours. $\times 390$. FIG. 7 *a*, *b*, *c*. Types of anastomosis. $\times 1850$. FIG. 8. Detail of eight variously derived hyphal strands and their anastomosis. Not all of the conidial sources are illustrated. $\times 900$. FIG. 9. Hyphae and conidiophores from a single spore, 48 hours. $\times 390$. FIG. 10. Septal pores between cells. $\times 1850$. All figures drawn with the aid of an Abbé camera lucida.



ture hyphae, producing a microscopic picture of much interlacing (figs. 6, 7). The total effect is of large clumps of spores as foci from which radiating hyphae fuse freely amongst themselves (fig. 8). Nuclear descendants of many spores thus have possible introduction into the mature hyphae. In figure 8 at least eight spores and their hyphal outgrowths are confluent. The nuclei divide very freely and their passage from one hypha to another is easily demonstrated (fig. 7). This free movement in the hyphae is greatly facilitated by the infrequency of septa in the oldest regions of the mycelium (those nearest the spores). In the septate areas the nuclei possibly could migrate from cell to cell through septal pores. These can be demonstrated by the chlor-zinc-iodide and I_2KI method, although they are very fine and difficult to show (fig. 10). Any significance that might be attached to a plurinucleate condition of the conidia is diminished when it is apparent that a random assortment of nuclei from various conidial sources is so easily obtained in the hyphae.

Each uninucleate conidium receives a daughter nucleus from the original nucleus of the phialide, itself a descendant of any nucleus in the mycelial network producing the conidiophore. If there are any factorial differences in the nuclei of the mycelium their allotment to the conidium-producing cells is certainly random as a result of anastomoses, and consequently conidia from the same fertile hypha could carry different nuclear factors. Likewise if a single conidium with a single nucleus is germinated to produce mycelium and conidiophores it is obvious that the first conidial descendants all have nuclei exactly alike, borne on a mycelium without anastomoses. That a single spore if germinated by itself can produce conidiophores and conidia is not difficult to show (fig. 9). Subsequently these conidia in turn will germinate to increase the colony by more hyphae which then may anastomose. However, the nuclei will all be identical, unless somatic mutation occurs. In watching individual spores widely spaced on agar films, it was evident that these spores with no chance to develop anastomoses germinated much more slowly and less vigorously than those sown in large numbers.

A survey of the literature reveals very few cytological descriptions of *Penicillium*. Thom (1930) recognizes the phenomenon of anastomosis in the genus and cites Dangeard's work on the cytology of certain species. The identity of Dangeard's species may not be clear today, but there can be no doubt that as early as 1907 he described a *Penicillium* (*P. vermiculatum*) with uninucleate spores and mycelium (see his plate 17, figures 10 and 11), and that this species also exhibited frequent anastomoses. He describes the fusion of the anastomosing cells, the resorption of the walls at those points, and the subsequent nuclear passage. In another species (*P. crustaceum*) he notes that the thallus cells are plurinucleate, but that they become uninucleate in the conidiophore. Conidium formation he likens to the budding

of yeasts, each conidium receiving a daughter nucleus prior to the formation of a basal wall. Dangeard's papers still represent the most complete cytological series available.

Anastomoses among germinating hyphae in *Penicillium* were recognized in 1893 by Wehmer who described them for *Penicillium luteum*. Anastomosis in other Ascomycetes has been noted as early as 1870 by de Bary and Woronin in two species of *Sordaria*. The Tulasne brothers illustrated the same behavior in *Cryptospora aucta*. Their comments have several points of interest in connection with *Penicillium notatum* and its anastomoses. The Tulasnes mentioned that those germ tubes which had been growing for a long time formed septa and that the young germ tubes coalesced with each other or with the conidia themselves so that "wonderful anastomoses" arise (Grove *et al.* 1931). Biourge (1923) illustrates various species of *Penicillia* without particular reference to their nuclei. Some of his figures of spores and cells suggest that these are uninucleate,—one may be binucleate—but no such statement attends the figures. Probably there are both uninucleate and plurinucleate species of the genus.

Some species of *Penicillium* produce an ascocarpic or zygotic stage, but this type of reproduction is unknown for *P. notatum* Westling, and consequently the combination and segregation of hereditary factors through karyogamy and meiotic division cannot be shown by genetic experiments as it can in some fungi (e.g., *Venturia inaequalis*, Keitt 1941; *Hypomyces solani* f. *cucurbitae*, Hansen and Snyder 1943). However, beginning with the work of Hansen and Smith in 1932 there has been serious consideration of the problem of variation in imperfect fungi. Hansen has introduced the term "dual phenomenon" to explain the means of variation in these azygotic fungi. In 1938 Hansen described the results of single-spore isolations from "multinucleate, binucleate, and mainly uninucleate" spores. The last category is the one in which *P. notatum* would fall. From his multinucleate single-spore cultures he found three types of variants were produced: two contrasting types, the homotypes, and their intermediate types, the heterotypes. The latter consistently give rise to more heterotypes and the former reproduce themselves. This dual phenomenon is due to heterokaryosis, or the possession of two genetically unlike kinds of nuclei in the cells. Their separation results in homotypes. It is easy to see how this operates in multinucleate spores—the phenotypic expression of the dual phenomenon is the result of the different genotypic nuclei present in them. If all the nuclei in a spore are genotypically identical then a homotype results. Differences in balance between the two nuclear types gives different phenotypic heterotypes. In uninucleate lines Hansen also isolated two homotypes (*Verticillium albo-atrum*) but it took many cultures—up to 50—to produce a line with the two homotypes together in the same spore. He assumed that these spores then are

binucleate. Consequently in maintaining such a fungus by single-spore transfer the chances of selecting a spore containing both homotypes is extremely small. Unless that particular kind of a spore is transferred the subculture will carry only one of the homotypes. Hansen feels that the occurrence of the dual phenomenon is frequent enough to warrant regarding it as the natural condition in imperfect fungi.

Post (1933) from single-spore cultures of *Macrophomina Phaseoli* derived two lines, one with and one without pycnidia. In *Penicillium notatum* the particular factorial difference under consideration is physiological: the penicillin-producing capacity. The means by which heterokaryosis is established in this fungus have already been shown. The cytogenetic behavior easily allows for the presence or absence of differing factors in the mycelium and consequently among the spores. Hansen (1942) remarks that heterokaryosis cannot occur in uninucleate cells. Such a conclusion is obvious, but if the nuclear behavior is such as to allow for genetic differences among spores even if not in them, then the ultimate effect achieved through subsequent anastomoses of the hyphae from these spores is the same. To support this reasoning a quotation from Hansen (1942) seems appropriate: "In this connection it is well to remember that at least two factors or mechanisms operate against the possibility of the uninucleate condition being continuous or permanent in any fungus. Those two factors, mitosis and anastomosis, operating singly or together are able to produce binucleate, trinucleate, and quadrinucleate cells in fungi generally considered to have uninucleate cells."

In *Penicillium notatum* the random assortment or mixing of nuclear types in the mycelium produces the effect of heterokaryosis even though the septate portions of the thallus are uninucleate. Dodge (1942) has discussed the effect of the inclusion of different sets of genes in the same cytoplasm but not in a common nucleus. The dissociation of homotypes from the dual condition can be concerned with physiological or morphological differences. Their association produces heterokaryotic vigor.

Therefore the trouble with single-spore transfers of *Penicillium notatum* is due to the fact that such practice does carry on a pure line but presumably a homotypic and not a heterotypic one. And the maintenance of the incomplete nuclear line is undesirable. By perpetuating the homotypes together or assuring heterokaryosis, the desired strain can be maintained. In *Penicillium notatum* this is done easily by mass spore transfer which assures an abundance of anastomosing hyphae and a recombining of the homotypes.

SUMMARY

1. Conidia of *Penicillium notatum* West. are uninucleate. They germinate by one or two germ tubes.

2. Anastomosis occurs freely among spores and hyphae, accompanied by nuclear division and nuclear migration.

3. The assimilative hyphae are plurinucleate or binucleate, becoming uninucleate in the cells subtending the conidiophores. Phialides are uninucleate.

4. The anastomosing of hyphae and spores in multiple spore transfers assures a combining of factors and heterokaryosis as spores with nuclei of different origins are brought together.

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BRAZILIAN CHYTRIDS—I. SPECIES OF NOWAKOWSKIELLA

JOHN S. KARLING

While serving as Field Director of the exploration department of the U. S. Government's Rubber Development Corporation in Brazil during 1943, the author had unlimited opportunities to collect soil and water samples for study of the aquatic fungi of the Amazon Valley. Inasmuch as nothing is known about the aquatic fungi of this vast tropical area, it seemed highly worth while to the writer to utilize this opportunity, although he was primarily engaged in exploring the Brazilian jungles for untapped sources of wild rubber. Soil and water samples were collected from swamps, small streams, lakes, and rivers in various localities and sent to central headquarters in Manaus, Amazonas, where they were baited with bits of young corn leaves, thin onion skin, cellophane, hemp seeds, and other favorable substrata. These samples were examined and studied in a preliminary manner at Manaus as time and opportunity permitted and were later sent to Columbia University for further culture and intensive investigation.¹

Among the numerous chytrids discovered and cultured in this manner were five species of *Nowakowskiella*: *N. ramosa*, *N. elegans*, *N. profusa*, and two additional species which appear to be new. The first of these new species is distinguishable by an unusual type of sporangium dehiscence and by zoospores which contain numerous small granules instead of a single large refractive globule like other species of *Nowakowskiella*. For this reason it is named *N. granulata*. The second species is characterized primarily by elongate, clavate, cylindrical, septate or non-septate sporangia in addition to pyriform and spherical ones, and is accordingly designated as *N. elongata*.

***Nowakowskiella granulata* Karling, sp. nov.** Fungus saprophyticus; rhizomycelio profuso, copiose ramoso, juveni hyalino in aetate paulo fuscante et membranum crasso, partibus tenuibus 1.5-7 μ diametro, interdum reticulatis, incrementis pluribus plerumque non septatis, ovalibus 6-8 \times 9-11 μ , vel late fusiformibus 5-9 \times 8-13 μ , vel prope globosis 6-10 μ diametro, vel irregularibus; sporangiis terminalibus intercalariisve, plerumque non apophysatis, globosis 12-35 μ diametro, vel piriformibus 12-22 \times 15-30 μ , vel ovalibus 10-18 \times 12-25 μ , vel interdum irregularibus, 1-3 papillas efferentes 3 \times 5 μ , vel 1 plurave collos elongatos habentibus; papillae efferentis apice canaliculisve maturis mollescentibus obturaculum opacum in ore facientibus, protoplasmati inter haec contracto et operculum sub obturaculo

¹ The writer is deeply grateful to Miss Anne M. Hanson and Miss Alfhild Johanson for receiving the water and soil samples and taking care of the cultures during his absence in Brazil.

faciente; operculis hypocrateriformibus cyathiformibusve, semiglobosis conicisve, 3–7 μ diametro; zoosporiis globosis 5–6.6 μ diametro, plura aureo-brunea grana capientibus, flagello circa 35 μ longo; sporis perdurantibus levibus hyalinis, membranum 1.5–2 μ crassis, globosis 15–24 μ , vel ovalibus 15 \times 20 μ , globulum refringens magnum (ad 12 μ diametro) cum pluribus parvis habentibus; germinatione non visa.

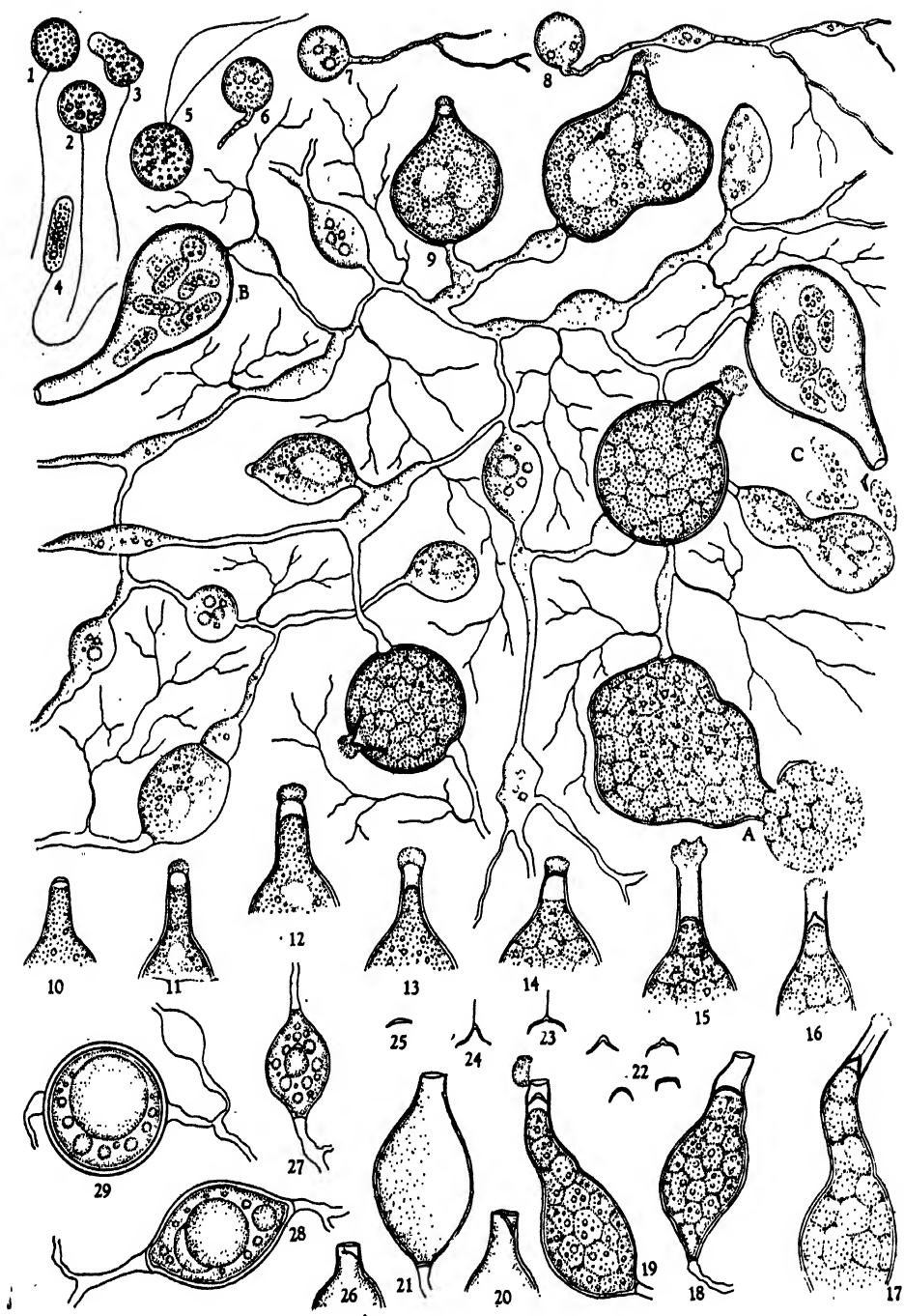
Saprophytic in decaying vegetable debris in Igarape San Carlos, Matto Grosso and Igarape Velho near Porto Velho, Amazonas, Brazil.

Nowakowskiella elongata Karling, sp. nov. Fungus saprophyticus; rhizomycelio hyalino, profuso, copiose ramoso, partibus tenuibus 1–6 μ diametro, interdum reticulatis, incrementis pluribus non septatis, ovalibus 5–13 \times 7–15 μ , vel late fusiformibus 4–8 \times 8–17 μ , vel globosis 5–15 μ , plerumque multos globulos refringentes capientibus; sporangiis terminalibus intercalaribusve, plerumque non apophysatis, septatis vel non, longe clavatis, 8–40 \times 20–820 μ , vel cylindricis apicem turgidis, curvis complicatisve rectisve, 5–20 \times 30–900 μ , vel piriformibus 15–44 \times 20–70 μ , vel globosis 10–70 μ diametro, vel ovalibus irregularibus; operculo circulari ovalique in extrema linea, hypocrateriformi, 4–8 μ diametro, rare permanente; zoosporiis globosis, 5–6 μ diametro, unico (rare duobus) globulo refringenti conspicuo 2–2.5 μ diametro habentibus; sporis perdurantibus plerumque intercalaribus ex incrementis ortis, hyalinis levibus globosis, 16–24 μ diametro, vel ovalibus, 14–16 \times 18–22 μ , magnum globulum refringentem a globulis parvioribus tabulatim circumdatum habentibus, germinantibus ut prosperangiis, parte interiori emergente ut zoosporangio membranam tenui ad superficiem sporae.

Saprophytic in decaying vegetable debris from Rio Negro and swamps at Flores Nabuco near Manaus, Amazonas; in soil samples from Campo Grande, Matto Grosso, and Rio Madeira near Porto Velho, Amazonas, Brazil.

NOWAKOWSKIELLA GRANULATA

As has been noted elsewhere, this fungus differs primarily from other species of *Nowakowskiella* by its unusual type of sporangium dehiscence and granular content of the zoospores. As is shown in figure 1, the latter are spherical and lack the single large refractive globule which is so characteristic of other species of this genus. Instead, the refractive material is usually dispersed in the form of numerous small golden-brown granules of fairly uniform size, which impart to the protoplasm a typical granular appearance. Sometimes, however, the granules may coalesce and form several larger refringent globules (figs. 2–5). The method of emergence from the sporangium (fig. 9 A), subsequent behavior at the exit orifice, and type of motility of the zoospores, on the other hand, are essentially similar to those of other species of *Nowakowskiella*. They may frequently become amoeboid (fig. 3) and creep about as elongate rods (fig. 4). Such shapes are common for spores remaining in the sporangia after the latter have opened (fig. 9 B, C). Large biflagellate zoospores are occasionally formed as the result of unequal or incomplete cleavage (fig. 5).



The type of zoospore germination (figs. 6-8) and the development of the thallus are fundamentally similar to those of other species of *Nowakowskiella* and *Cladochytrium* described by Berdan (1941), Hillegas (1941), and other workers and need not be emphasized in detail here. It is to be noted, however, that as the zoospores come to rest and germinate, the refractive granules aggregate and coalesce to form from two to seven larger refringent globules. Figure 9 shows a portion of the rhizomycelium of *N. granulata* with its spindle organs, rhizoids, and sporangia in various stages of development and maturation.

Particularly different from other species, however, is the manner of sporangium dehiscence and the changes involved in operculum development. In all other known members of *Nowakowskiella*, the operculum is formed at the tip of the exit papilla or canal and is pushed up as the zoospores emerge, whereas in *N. granulata* it is usually formed at varying depths within the papilla or exit canal. The successive stages of this process are shown in figures 10-19. In the early stages (fig. 10) the tip of the exit tube looks like that of any other operculate species, but within a few hours it begins to soften and swell (fig. 11) so that a plug of opaque material is eventually formed at the apex. At the same time the more granular and heterogeneous protoplasm in the neck usually recedes downward, leaving a hyaline area of varying size beneath the plug. This area appears to be filled with a hyaline, more or less viscid substance. At first the surface of the granular protoplasm in the tube is concave (fig. 11), but with further development it becomes convex (fig. 12). Figure 12 shows a later stage in which the opaque plug has increased in size, while the granular protoplasm has receded further and become convex on its surface. Sporangia in this stage of development are strikingly similar to those of *Cladochytrium hyalinum* and *C. crassum* described by Berdan (1941) and Hillegas (1941)—so much so that, until the formation of the operculum had been observed, the author regarded the

Explanation of figures 1-29

Nowakowskiella granulata. FIGS. 1-4. Spherical, amoeboid and elongate zoospores with finely granular contents. $\times 3100$. FIG. 5. Giant biflagellate zoospore. $\times 3100$. FIGS. 6-8. Germination of zoospores. $\times 3100$. FIG. 9. Portion of the rhizomycelium showing developmental stages of the sporangia. $\times 2800$. FIGS. 10-14. Successive stages in the deliquescence of the tip of the exit tube, formation of a plug of opaque substance, and the development of sunken opercula. $\times 2800$. FIGS. 15, 16. Plugs of opaque substance extending down into the tube to sunken opercula. $\times 2800$. FIG. 17. Longitudinal section of sporangium with a cone-shaped operculum capped by a fine filament. $\times 2800$. FIG. 18. Section of a sporangium with empty exit canal above operculum. $\times 2800$. FIG. 19. Plug of opaque substance displaced and adhering to tip of exit canal. $\times 2800$. FIG. 20. Empty sporangium showing region of attachment of operculum in exit canal. $\times 2800$. FIG. 21. Persistent operculum in exit canal. FIGS. 22-25. Variations in size and shape of opercula. $\times 3100$. FIG. 26. Sporangium with a very thin, frayed, persistent operculum. $\times 2800$. FIG. 27. Early stage of resting spore development. FIGS. 28, 29. Mature resting spores. $\times 2800$.

present fungus as a species of *Cladochytrium*. In figure 13 an increase in size of the opaque plug and further recession of the protoplasm are evident. This figure also shows the first indication of operculum development at the surface of the receded granular protoplasm in the form of a cup-shaped thickened layer. Apparently further thickening of the bounding or plasma membrane occurs until a well defined operculum is formed (figs. 14-18).

Slight variations of the above described process often occur. Recession of the granular protoplasm in the neck may be very slight or even lacking so that the operculum develops immediately beneath the plug (fig. 14). In such instances recession may sometimes take place after the operculum is formed with the result that the hyaline area may occur between the operculum and sporeplasm. Sometimes the opaque substance may extend down into the exit tube to the operculum, as is shown in figures 15 and 16. In a few sporangia observed the opaque material had apparently deliquesced completely, leaving the exit tube empty above the operculum (fig. 18). In two instances the plug was uplifted more or less intact, displaced, and attached to one side of the exit canal (fig. 19), although the zoospores and sunken operculum had not emerged. Normally, however, the operculum and plug are pushed out simultaneously as the zoospores emerge.

As has been noted in the diagnosis above the opercula are oval or circular in outline and shallow saucer-, bowl-, cup-, and cone-shaped (figs. 22-25). Sometimes they may be distinctly apiculate (fig. 16) with the apex capped by a tenuous spine of hyaline material (figs. 17, 23, 24). Oftentimes the operculum does not separate flush with the inner wall of the exit canal but leaves an inward projecting ring of wall material, which in longitudinal section looks like two short sharply-pointed ledges (fig. 20). A few sporangia have been observed in which the operculum was persistent inside the exit tube (fig. 21). Figure 26 shows a sporangium with an operculum which is very delicate, thin and frayed at the edge. In such cases the operculum may be so thin that it can be seen only with difficulty, and the sporangia accordingly appear at first sight to be inoperculate.

The occurrence of such poorly defined opercula and the presence of the *Cladochytrium*-like plugs of opaque material in the exit orifices (figs. 12-17) suggest the possibility that an evolutionary transition from inoperculate cladochytriacous species to operculate ones or vice versa may have occurred through dehiscence changes of the nature described above. In that event *N. granulata* may possibly be regarded as a transitional species.

Only a few resting spores have been observed in *N. granulata*. They are usually formed from the intercalary swellings which increase in size, develop an abundance of refractive substance (fig. 27) and become thick-walled. With further development, most of the refringent globules coalesce and form one or two large central ones which may be surrounded by a layer of

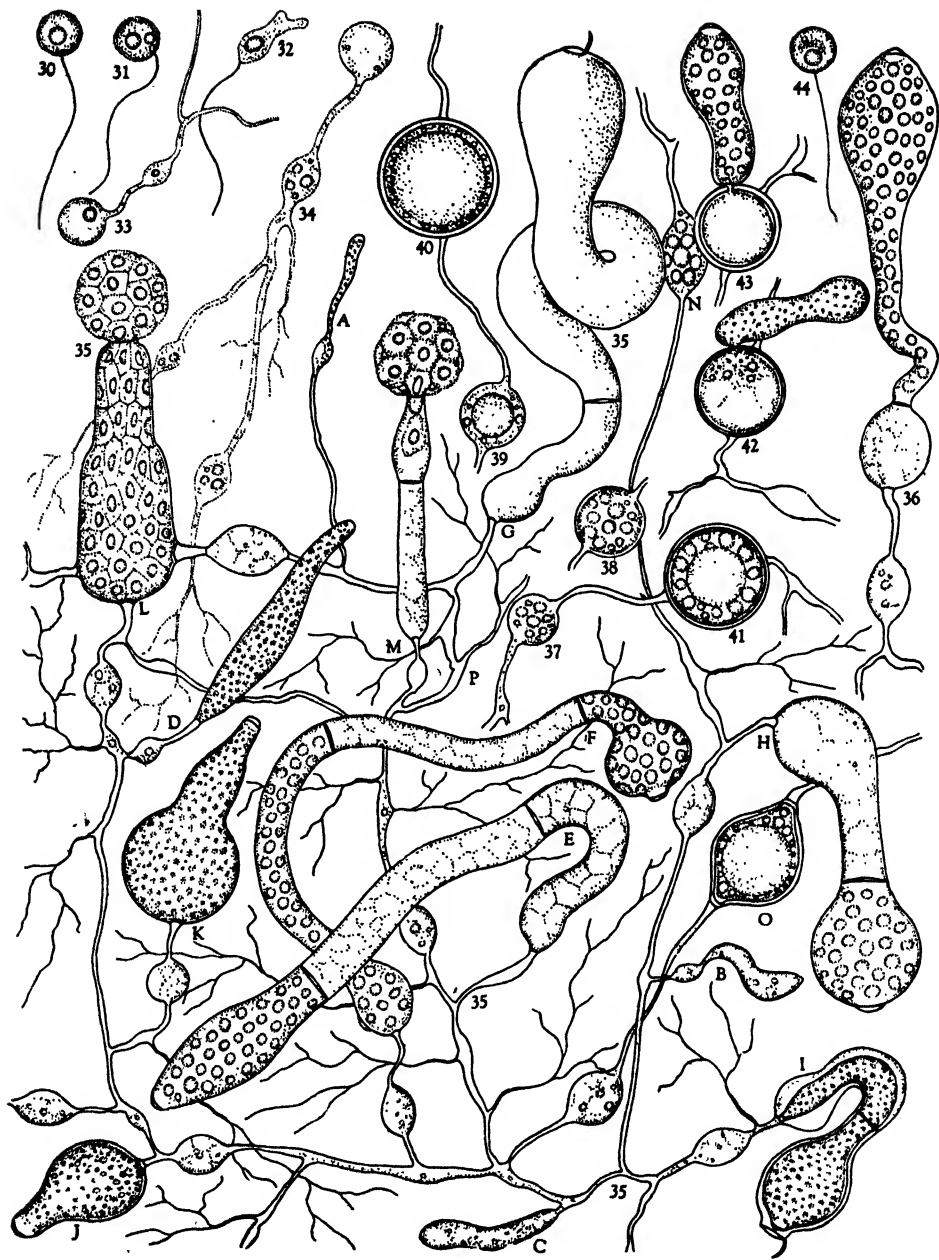
smaller globules. As is shown in figures 28 and 29, the resting spores may be oval, citriform, and spherical in shape. So far, no germination stages have been observed.

NOWAKOWSKIELLA ELONGATA

This species has been collected in the northern and southern parts of Matto Grosso and in Amazonas near Manaus in moist soil as well as water samples. It usually crops up in great abundance in cultures baited with corn leaves and onion skin, and as far as present observations go, it appears to be more widely distributed and ubiquitous than *N. granulata*. Its essential structural characters and developmental phases are illustrated in figures 30-43. Except for the sporangia, the rhizomycelium of *N. elongata* resembles more closely that of *N. elegans* than any of the other species of *Nowakowskiella*. Its zoospores are of the same size and contain one or rarely two conspicuous refractive globules (figs. 30-32). They may likewise become amoeboid (fig. 32), creep around, and then round up and dart off. No fundamental differences in zoospore germination (figs. 33, 34) and development of the rhizomycelium have been observed in this species, and consequently it would be superfluous to describe these developmental phases in detail. The present description will accordingly be confined to the principal structural differences.

A portion of the rhizomycelium with its variously-shaped sporangia, broadly oval spindle organs, rhizoids, and resting spores is shown in figure 35. The most striking structures in this figure are the elongate, clavate and cylindrical sporangia (figs. 35 E, F, G, H, I, 36). These sporangia are so similar to those of *Cylindrochytridium* (Karling 1941a) that, until the polycentric rhizomycelium had been observed, the author believed that they were related to this monocentric genus. As was noted earlier, the sporangia may be straight, curved, or coiled, non-septate or with one to three septa. The apical end in which the spores are formed is usually inflated or swollen. The base of the sporangium may also be slightly inflated, as is shown in figures 35 F, G, H, I, and 36. Figure 35 F shows an exceptional sporangium in which the zoospores were formed in both the basal and apical ends with a sterile vacuolate segment in the center. Not all sporangia, however, are elongate, clavate, and cylindrical. They may also be spherical, pyriform, flask-shaped, and irregular. Figures 35 J and K show two pyriform sporangia, while the one illustrated in figure 35 L is intercalary and flask-shaped with rhizoids arising from the sides as well as the base. In contrast to those of *N. elegans*, these sporangia are rarely apophysate. Instead, they are usually subtended by a short tenuous filament which leads to an intercalary swelling or spindle organ (figs. 35 F, I, 36).

Stages in the development of the elongate sporangia are shown in figures 35 A, B, C, and D. Such sporangia usually begin as elongate clavate swell-



ings at the tips of the rhizomycelium (fig. 35 F) which increase in length and diameter (figs. 35 B, C) and are soon delimited by a cross septum from the remainder of the thallus (fig. 35 D). At first the protoplasm is dense and greyish-granular, but as development progresses, vacuoles appear and the refringent granules gradually coalesce into larger globules. As the sporangium elongates and the denser protoplasm gradually moves toward the apex, the basal portion becomes more and more vacuolate and is eventually delimited by a cross wall. If further elongation occurs, the process is repeated along the length of the sporangium, and secondary and tertiary septa are formed. In the sporangium shown in figure 35 F movement of the denser protoplasm was apparently toward both ends, so that the central portion became vacuolate and was cut off by cross walls. The dense protoplasm in the apex soon undergoes cleavage into zoospores which eventually push off the operculum, emerge, and form a globular mass at the exit orifice (figs. 35 L, M). The subsequent behavior of the zoospores is essentially similar to that of other species of *Nowakowskiella*.

Resting spores occur rather commonly in old cultures of *N. elongata*, and as in the previously described species, they are usually formed by the growth and transformation of spindle organs. The early developmental stages may be easily recognized by an increase in the number and size of the refractive globules in the intercalary enlargements (figs. 35 N, 37). This increase continues as the enlargements grow in size (fig. 38), and gradually the globules coalesce to form a large central or excentric one. The wall continues to thicken in the meantime until the large oval, citriform, or spherical resting spore is fully formed (figs. 35 O, 40, 41). Particularly conspicuous is the size of the larger refractive globule in the mature spore. As has been noted elsewhere, it may be up to 15 μ in diameter and in some cases almost completely fills the spore. When smaller in size, it is usually surrounded by one or two layers of small globules (fig. 41).

So far, only a few germination stages have been observed. In this process the content of the spore emerges through a pore in the wall and forms a thin-walled evanescent zoosporangium on the surface as in other chytrid species. Figures 42 and 43 show late progressive developmental stages of small elongate sporangia, but more elongate and septate sporangia also have been observed.

Explanation of figures 30-44

Nowakowskiella elongata. FIGS. 30, 31, 32. Spherical and amoeboid resting spores. $\times 3100$. FIGS. 33, 34. Germinating spores. $\times 3000$. FIG. 35. Portion of the rhizomycelium showing variations in the shape and structure of the sporangia. Hyphal anastomosis at p. $\times 2800$. FIG. 36. Clavate sporangium with inflated base. FIGS. 37-39. Stages in the development of resting spores from spindle organs. $\times 3000$. FIGS. 40, 41. Mature resting spores. $\times 3000$. FIGS. 42, 43. Germinating resting spores. $\times 2800$. FIG. 44. Zoospore from germinated resting spore. $\times 3100$.

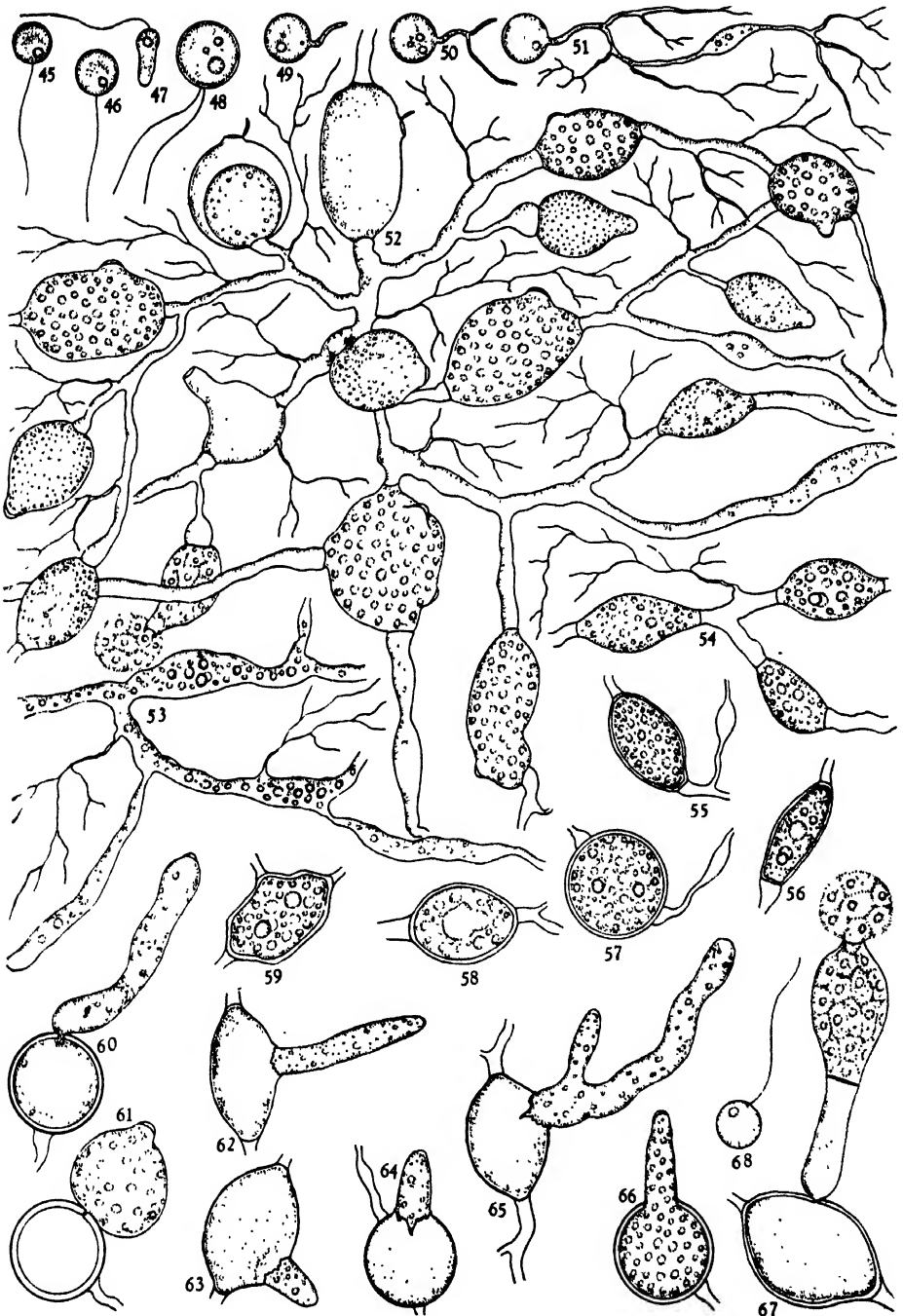
NOWAKOWSKIELLA PROFUSA

This species was discovered by the author in New Kent County, Virginia, in the winter of 1941, and later (1941a, 1942) collected in Texas, Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, South Carolina, and Tennessee. It appears thus to be widely distributed in the southern states, and consequently it was not surprising to discover its occurrence in South America also. So far, however, it has been found in only one locality in Brazil—in a moist soil sample at San Carlos on the Madeira-Mamore railroad in Matto Grosso.

Inasmuch as *N. profusa* has been only briefly described and never illustrated, a short description with figures of its chief structural characters and developmental stages is herewith presented from the Brazilian material. No fundamental differences between the South American and North American material has been found, so that the present account holds for both types. *Nowakowskiella profusa* differs principally from the other known species of this genus by its smaller zoospores, the rare occurrence or even lack of well-defined spindle organs, and yellowish-brown resting spores which may function directly as sporangia with exit canals in germination or act as prosporangia and give rise to thin-walled zoosporangia on their surface. The comparatively smaller zoospores and their more minute refractive globules are illustrated in figures 45–47. They germinate (figs. 49–51) and give rise to a tenuous rhizomycelium in the same manner as in the previously described species. The fully developed and mature thallus is relatively coarse, and has the appearance and structure of the portion shown in figure 52. An abundance of intercalary oval, elongate, and spindle-shaped sporangia with one or more apical, subapical, or lateral opercula is common and distinctive in this species. Particularly characteristic is the rare occurrence per se or lack of sharply defined relatively empty spindle organs of the type found in *N. granulata*, *N. elongata*, and other cladochytriacous species. Intercalary swellings frequently develop, but they usually increase in size and become sporangia or resting spores. In a previous publication (1941a) the author reported that the tenuous portions of the rhizomycelium vary from 6 to 15 μ

Explanation of figures 45–68

Nowakowskiella profusa. FIGS. 45–47. Spherical and amoeboid zoospores with single small refractive globule. $\times 3100$. FIG. 48. Giant biflagellate zoospore with three refractive globules. $\times 3100$. FIGS. 49–51. Germination of zoospores. $\times 3100$. FIG. 52. Portion of the rhizomycelium. $\times 2800$. FIG. 53. Portion of an older rhizomycelium with numerous refractive globules. $\times 300$. FIG. 54. Early stages in resting spore development. $\times 2800$. FIGS. 55–59. Variations in size and shape of resting spores. $\times 2800$. FIGS. 60, 61. Longitudinal views of resting spores which are functioning as prosporangia in germination. $\times 2800$. FIGS. 62–65. Surface views of resting spores which are germinating directly as sporangia with exit tubes. $\times 2800$. FIG. 66. Similar resting spore in longitudinal view. $\times 2800$. FIG. 67. Septate sporangium from germinated resting spore with emerging zoospores. $\times 2800$. FIG. 68. Zoospore from germinated resting spore. $\times 3100$.



in diameter. Subsequent study of additional North American as well as South American material has shown that the larger diameters are very exceptional and that the more normal range is from 1 to 9 μ .

Resting spores occur very abundantly in *N. profusa* and germinate after a short rest period. As cellophane and corn leaf cultures of this species become older, a marked increase in the amount of refractive substance usually occurs in the rhizomycelium (fig. 53). This change is usually, but not always, indicative of resting spore development. In such thalli the refringent globules accumulate in the intercalary swellings, which later become delimited from the more tenuous empty portions of the rhizomycelium by cross walls (fig. 54). These segments are the incipient resting spores. With further growth and increase in size, aggregation of refractive globules, and thickening of the wall they finally attain maturity. Unlike those in the spores of the previously described species, however, the refringent globules rarely coalesce to form a large central one. Instead, they usually remain comparatively small and evenly distributed (figs. 55-57, 58). With increasing age, the wall of the spore turns yellowish-brown in color. As has been reported earlier (1941a), the mature spores may be elongate, fusiform, truncate, oval, spherical, and slightly irregular in shape.

In germination, as noted earlier, they may function as prosperangia or directly as sporangia. In the former case, the content emerges through a relatively small pore in the wall and develops into thin-walled zoosporangia of various sizes and shapes, as is shown in figures 60, 61, and 67. Germination of this type has not been observed very often, and so far it appears to be somewhat exceptional. In the second type an exit tube bursts through the wall as the content of the spore is transformed directly into zoospores. Figures 62-65 show surface views of such spores with the protruding exit tubes, while figure 66 illustrates a similar spore in longitudinal section. The exit canals vary considerably in diameter and length and may occasionally branch (fig. 65). Especially noteworthy in figures 62-65 are the large jagged openings made in the spore wall by the protruding tubes. The types of germination herein described are not always sharply differentiated and transition stages between the two frequently occur. Regardless of the type, posteriorly uniflagellate zoospores are eventually produced as is shown in figures 67 and 68.

NOWAKOWSKIELLA RAMOSA

This species was first observed by Butler (1907) in rotting stems of *Triticum vulgare* in India and later reported as *N. endogena* by Domjan (1936) in decaying leaves of *Typha* from Hungary. It was subsequently found in the New World by the author (1941a, 1942) in decaying vegetable debris from Texas, Alabama, Florida, Louisiana, and South Carolina. The

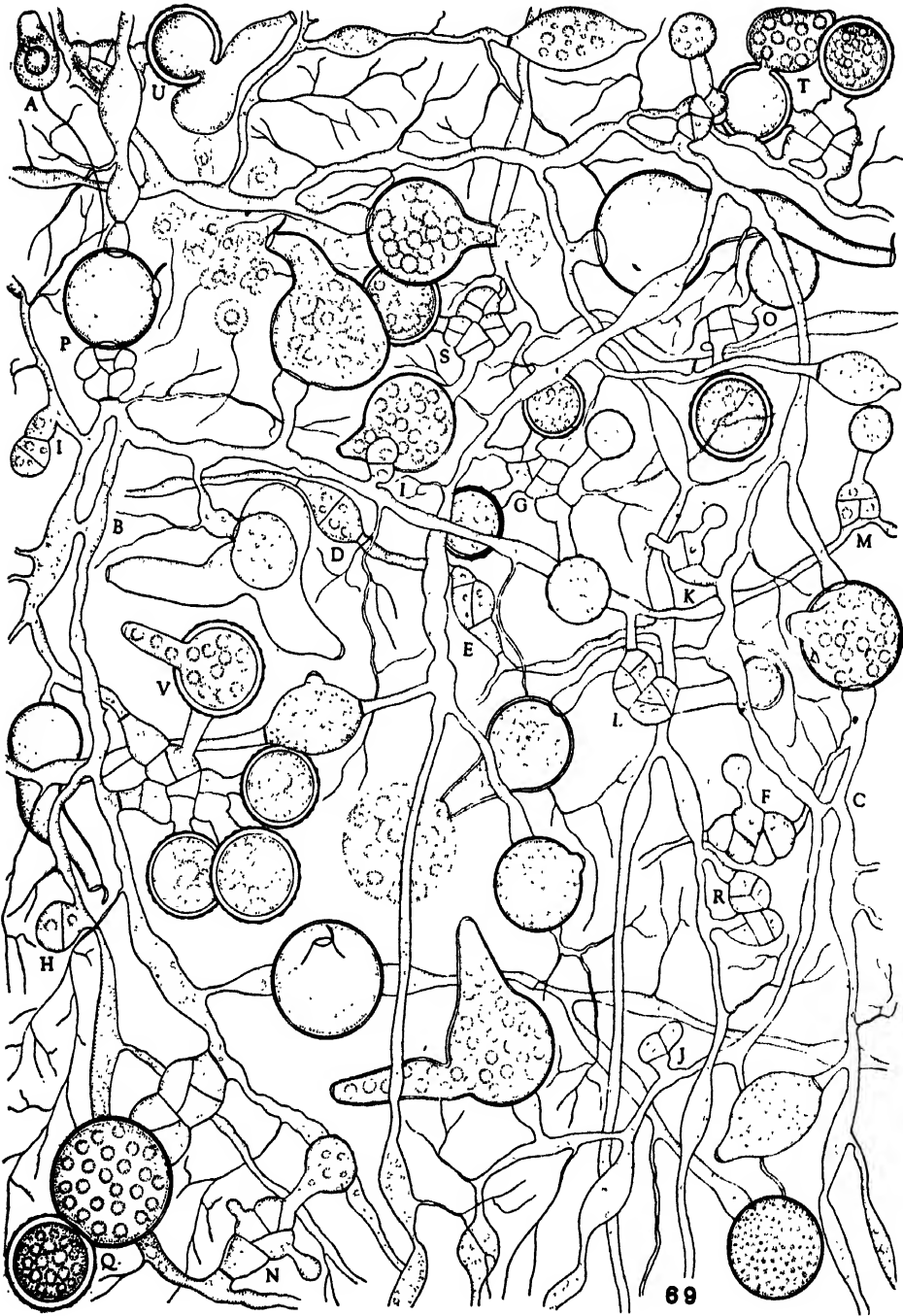
discovery of its presence in decaying grass leaves from a swamp near San Carlos, Matto Grosso, Brazil, shows that it is even more widely distributed. Study of the South and North American material has completed our knowledge of the life cycle of this species, and it is now possible to complete the species diagnosis begun by Butler in 1907.

N. RAMOSA Butler. Rhizomycelium hyaline, profuse, richly-branched, occasionally septate; tenuous portions $1.5-8\ \mu$ in diameter, occasionally anastomosing; spindle organs oval $4-6 \times 6-10\ \mu$, or broadly fusiform $5-7 \times 12-16\ \mu$, or almost spherical $6-9\ \mu$, or elongate. Sporangia terminal or intercalary, apophysate or non-apophysate, apophysis when present usually subspherical and up to $11\ \mu$ in diameter; sporangia spherical $20-50\ \mu$, or pyriform $15-30 \times 25-40\ \mu$, or oval $15-20 \times 22-30\ \mu$, or elongate or slightly irregular, with 1-3 low exit papillae or exit tubes up to $100\ \mu$ long. Opercula oval or circular in outline, $4-6\ \mu$ in diameter. Zoospores spherical $6.6-8.8\ \mu$, with a large ($3\ \mu$) plastic refractive globule and a flagellum $36-40\ \mu$ long; frequently becoming amoeboid; forming a globular mass at the exit orifice immediately after emerging but soon separating and dispersing. Resting spores formed from proliferated spindle organs and short lateral branches; spherical or slightly angular, $15-26\ \mu$, hyaline to yellowish in color, with numerous small refractive globules or a large central one surrounded by smaller globules; wall $1.8-2.6\ \mu$ thick, smooth or slightly verrucose (?); resting spores usually functioning as prosperangia in germination and giving rise to thin-walled zoosporangia on their surface; occasionally germinating directly as sporangia with an exit tube which bursts through the spore wall.

Saprophytic in decaying leaves of *Triticum vulgare* in India (Butler 1907), leaves of *Typha angustifolia* in Hungary (Domjan 1936), grass leaves and vegetable debris in the U.S.A. (Karling 1941a, 1942) and Matto Grosso, Brazil.

Nowakowskiella ramosa differs chiefly from the other known species of this genus by a marked proliferation of cells in relation to resting spore formation, and since the time of its discovery by Butler the question of whether or not sexuality is involved in this process has often been raised. For this reason particular attention has been given to this developmental phase in the Brazilian material. Inasmuch as the rhizomycelium and resting spore development of *N. ramosa* have not been extensively figured, a portion of the thallus with numerous developmental stages is presented in figure 69. When grown on cellophane the rhizomycelium may become very profuse and form a dense web of filaments, sporangia and resting spores, particularly at the edge of the substratum. Quite often almost the entire developmental cycle can be observed within a small area. Figure 69 shows a portion of such an area and illustrates very well the dense growth which this species may make.

No fundamental differences have been found between the North and South American material, except that in the latter the tenuous portions of



the thallus are often slightly coarser and more irregular. The difference, however, is not sufficiently great to warrant species differentiation. In both types of material the older filaments become fairly thick-walled with age. Hyphal anastomosis occurs fairly often (figs. 69 B, 69 C) as in other species of *Nowakowskiella*, but these fusions do not appear to have any sexual significance. At least they do not lead to the formation of zygotes.

As Butler and the author (1941a) have already reported, the resting spores of this species are formed from masses of proliferated cells in various portions of the rhizomycelium. In the Brazilian material they usually develop from spindle organs which undergo extensive proliferation. The initial stage in this process is shown in figure 69 D of an intercalary swelling which has divided transversely. Later tangential and longitudinal divisions also occur, so that the spindle organs become pseudoparenchymatous and irregular (figs. 69 E, 69 F). In the latter figure one of the cells has put forth a small stalked bud which is beginning to enlarge at the tip and will become a resting spore. A more advanced stage is shown in figure 69 G of an irregular spindle organ situated near the end of a filament and which bears two mature and two young spores. Most spores are borne on distinct stalks of varying length, and may sometimes appear in clusters up to six in number. At this point it is important to note that the development of resting spores from proliferating spindle organs is not restricted to *N. ramosa*. Similar but less extensive proliferation has been found by Berdan in *Cladochytrium hyalinum*, but in the latter species the spores apparently are not borne on stalks.

In addition to developing from spindle organs, the resting spores may also originate from short lateral branches which enlarge at their tips, divide, and undergo similar proliferation. Figures 69 H–N show various stages in this process and indicate that it is fundamentally the same as in the case of the spindle organs. Here also the spore rudiments begin as small stalked buds on the proliferating cells and develop into the mature spores (figs. 69 K, L, M). Occasionally, the proliferated lateral branches remain sterile and fail to form spores. Similar rare occurrences have been observed in the case of proliferated spindle organs also.

In this connection it may be noted that proliferation of the spindle organs and lateral branches may also be associated with the formation of

Explanation of figure 69

Nowakowskiella ramosa. A. Zoospore. $\times 3100$. B, C. Hyphal anastomosis. $\times 2800$. D, E, F, G. Stages in the origin of resting spores from proliferating spindle organs. $\times 2800$. H, I, J, K, L, M, N, O. Stages in the origin of resting spores from proliferating, short lateral branches. $\times 2800$. P. Cell proliferation in relation to sporangium development. $\times 2800$. Q. Proliferated lateral branch, the ultimate cell of which formed a resting spore, while the penultimate cell developed into a zoosporangium. $\times 2800$. R, S, T. Stages in the origin of resting spores from two short lateral branches which appear to have grown together and proliferated. $\times 2800$. U. Germinated resting spores which have functioned as prosperangia. $\times 2800$. V. Resting spore germinating directly with an exit tube. $\times 2800$.

zoosporangia as well. Figure 69 P shows an empty sporangium which apparently developed from one of the central cells of a proliferated intercalary enlargement. Another unusual growth is shown in figure 69 Q of a greatly enlarged phragmosporous branch, the ultimate cell of which formed a resting spore while the penultimate one developed into a zoosporangium.

In a few instances resting spores were observed to arise from two lateral branches which appear to have grown together and later proliferated (figs. 69 R, S, T). In the early developmental stages such branches resemble somewhat the isogametes of a homothallic Zygomycete, and this similarity has suggested that sexuality may be involved in resting spore development. Several developmental stages of this type have been carefully followed, but so far no cell fusion between contacting branches has been observed. It is not improbable that fusions may occur, but that they involve union of gametes is not at all certain. It is quite probable that they are vegetative and of the same nature as the hyphal fusions reported above. This view of the author is supported by the fact that zoosporangia as well as resting spores may result from such union as is shown in figure 69 S.

Regardless of the type of origin of the spores, a large amount of refractive material is usually formed in the proliferating cells and eventually accumulates in the spores as they mature. The refringent globules may coalesce to form a large central one or remain relatively small and evenly distributed. The mature spore of *N. ramosa* is predominantly spherical with a fairly thick wall. A large number of spores in the Brazilian material were uneven or slightly verrucose on their outer surface, but it is not certain whether this is a true wall character or merely an incrustation. A few slightly angular spores also have been found in this material, the discovery of which supports the author's (1941b) previously expressed view that the resting spores reported by Domjan as those of *N. endogena* in Hungary actually relate to *N. ramosa*.

The resting spores germinate readily under laboratory conditions, and in so doing they usually function as prosporangia, as in most other chytrids, giving rise on their surfaces to thin-walled zoosporangia as is shown in figures 69 T and 69 V. Sometimes, however, they may germinate directly as in *N. profusa* with an exit tube which bursts through the spore wall. Figure 69 V shows such a case with a fairly long operculate exit tube. The zoospores produced by the resting spores are similar in size, shape and behavior to those formed in the primary zoosporangia.

As was noted earlier, the type species of the genus, *N. elegans*, also was found in Brazil in a moist soil sample from San Carlos, Matto Grosso. This species is widely distributed in Europe and North America, and it was not surprising to find it in South America also. Inasmuch as it is well known and has been frequently described and illustrated, further description of it here

would be superfluous, particularly since no fundamental differences were observed in the Brazilian material.

The discovery of the new fungi, *N. granulata* and *N. elongata*, raises the number of species in *Nowakowskiella* to six. Of these, all have been found in Brazil except *N. hemisphaerospora* Shanor (1942). Careful search has been made for the latter species, but so far it has not appeared in any of the soil and water samples.

SUMMARY

Five species of *Nowakowskiella* have been found in various parts of the Amazon Valley, two of which, *N. granulata* and *N. elongata*, are new. The first of these two is distinguishable by sunken opercula in the exit papillae or tubes and zoospores which contain numerous small refractive granules instead of one large, conspicuous refringent globule. The other species is characterized primarily by elongate, straight, curved, or coiled, septate or non-septate, clavate and cylindrical as well as spherical and pyriform zoosporangia. *Nowakowskiella profusa*, *N. ramosa* and *N. elegans* also occurred in great abundance in various soil and water samples collected in Brazil.

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INTERESTING NORTH AMERICAN AGARICS

ALEXANDER H. SMITH

INTRODUCTION

During the summer and fall of 1941, with the aid of a grant from the Horace H. Rackham School of Graduate Studies of the University of Michigan, investigations of our western agaric flora were continued in four selected localities, the Payette Lakes region of west central Idaho, the Mt. Baker region in the northern Cascades of Washington, the Olympic Mountains of western Washington, and the McKenzie Pass region in central Oregon. The last half of July and first week in August were spent in the vicinity of Payette Lakes. Here, because of favorable conditions for the fruiting of fleshy fungi, intensive collecting was carried on in the ponderosa pine forests in the immediate vicinity of the lakes as well as in the balsam and spruce forests at higher elevations to the east and southeast. During August a location was selected a short distance above Glacier on the Nooksak River near Mt. Baker and trips were made into the mountains on either side of the river. During the early part of September, in company with E. B. Mains, a survey of the Baker River area was made from a location on Baker Lake. During the last of September and most of October intensive collecting was carried on in the northern Olympic Mountains of Washington, particularly in the vicinity of Olympic Hot Springs in the Olympic National Park, and on the slopes of Mt. Angeles near the town of Port Angeles. A final location was selected during early November at Sisters, Oregon, just east of the Cascade Mountains near McKenzie Pass. In this region the open forest of pine and larch furnished excellent collecting.

Because of exceptionally favorable weather conditions, good collecting was encountered at all of these stations, and many unusual fungi were found. Since the region around Payette Lakes in Idaho is ordinarily very dry during July and early August, it was an exceptional bit of good fortune to encounter both favorable collecting conditions and a luxuriant agaric flora at that time of year. The material gathered there becomes more interesting when one recalls that almost no information on the agaric flora of the Salmon and Payette River drainage is available. The comparison of this flora with that from similar plant habitats west of the Cascades is in progress.

The Olympic agaric flora of 1941 was outstanding particularly for the large number of *Cortinarii* it contained, and critical studies of many of these will be reported upon separately. Species of *Tricholoma* and *Clitocybe* were

also unusually abundant. The same relationships noted previously (Smith 1941) between the fungous and phanerogamic floras were verified during the fall of 1941. However, certain additional features were evident. The height of the season for *Cortinarius*, particularly those species not having viscid pilei, apparently follows the fruiting period of *Boletus Lakei*, *Gomphidius oregonensis* and the varieties of *Inocybe geophylla*. Species of *Clitocybe* appear to be equally abundant in the river valleys and along the ridges although a different series occurs in each of these habitats. One interesting feature of the fruiting pattern in 1941 was the superabundance of agarics in certain restricted localities, and the time of maximum fruiting in each locality. At the time *Cortinarii* reached the peak of their fruiting cycle on Mt. Angeles and in the Olympic Hot Springs district, there were very few agarics present in the Sol Duc River Valley only a few miles to the west. In the region around Olympic Hot Springs the most abundant fruiting occurred along the ridges and steep mountain slopes just east of the Hot Springs themselves. On previous expeditions, agarics were most abundant to the west about a half mile or more up Boulder Creek. In the alder and cedar flats in the river valleys below 1500 ft. elevation the peak of the fruiting cycle preceded that of the upper Canadian and Hudsonian life zones by about two weeks. *Russula*, *Cortinarius*, *Tricholoma*, *Clitocybe*, and *Mycena* were the characteristic genera in the latter regions and *Gomphidius*, *Clitocybe*, *Lepiota*, and *Rhodophyllus* were dominant in the former, although *Russula* and *Mycena* were also well represented.

The collecting in the Mt. Baker area of northwestern Washington was not as diversified as in the Olympic Peninsula, but this may have been an apparent rather than a real difference. Because of previous expeditions into the northern Olympics, little time was wasted there searching for favorable localities, and it was possible, because of the presence of an adequate system of roads, to reach all important habitats by auto and a few hours hiking. The opposite was true in the Mt. Baker region. Much more time had to be spent on the trail, with the result that survey work progressed slowly and a more limited number of habitats could be visited. The almost continuous rain added materially to the difficulty of collecting at elevations of 2500 ft. or more, and specimens carried for long distances were often damaged. As a result, relatively few collections were obtained here in comparison with the Olympics, but many interesting agarics were found and the collecting could not be classed as poor. *Russula* was the dominant genus at all elevations, and two species of *Mycena*, *M. atroalboides* and *M. clavicularis*, were the most abundant agarics. By the time we became established at Sisters, Oregon, the agaric season was fairly well along throughout the region west of the Cascades, but was about at its peak in the open pine country on their eastern slopes. Here an as yet undescribed *Mycena* liter-

ally covered the needles under *Pinus ponderosa*, and both *M. elegantula* and *M. laevigata* were regularly encountered on larch and pine logs and stumps. Species of *Clitocybe* were also encountered everywhere. In the forests at elevations of over 4000 ft. the agarics had already been badly frozen, and no study was possible. However, the conifer forests above this elevation in the vicinity of McKenzie Pass and Hogg Pass appear to be excellent agaric habitats in spite of the thin layer of needles and humus over the lava rock.

In the following account critical studies are presented for a few of the more interesting species collected during 1941 and a few additional agarics collected in other regions or at other times have been added. Unless otherwise stated the collection numbers are the writer's and the names of the colors within quotation marks are taken from R. Ridgway, *Color Standards and Color Nomenclature*, Washington, D. C. The names of colors not within quotation marks are used in accordance with the Ridgway system, but were not actually matched. This applies in particular to such common terms as tawny, ochraceous, avellaneous, and fuscous. The collections have all been deposited in the Herbarium of the University of Michigan.

THE GENUS AGARICUS

In a previous paper (Smith 1940) dealing with type specimens of American species of *Agaricus*, a number of Murrill's western species were omitted because the types had not been located. Since then a number of these have been found and studied with the result that certain rearrangements are necessary.

AGARICUS ABRAMSI Murrill, *Mycologia* 4: 298. 1912. The type is in very poor condition, but apparently represents a young specimen of a rather robust species. Its spores measure $5-6 \times 3-3.5 \mu$ and are identical with those of the species in the *A. silvaticus* complex in both size and shape. However, most of those found on the type were immature, as was evident from their pale color. The above measurements were made on the darkest spores present. No other distinctive features such as cheilocystidia or clamp connections were found. The eccentric stipe as given in the original description was very likely just an accident of growth. This species should be excluded from the genus because it is obviously based upon an abnormal specimen.

AGARICUS SUBRUFESCENTOIDES Murrill, *Mycologia* 4: 299. 1912. The type consists of an excellently preserved specimen. The pileus is covered with fine fibrillose scales, there are no remains of a fibrillose sheath below the annulus, and the spores measure $5-6.3 \times 3.3-3.8 \mu$. The carpophore appears to be typical of *A. silvaticus* in all respects. In my own collections of the latter there are some with less and some with more pronounced scales on the pileus.

The simple annulus, as described by Murrill, must be disregarded since that of the type is typically double. My first impression from reading the description of *A. subrufescentoides* was that it might be the same as *A. subrutilescens* (Kauff.) Hotson and Stuntz. However, the color of the pileus and the lack of any signs of a fibrillose sheath below the annulus rule out this possibility.

AGARICUS HONDENSIS Murrill, Mycologia 4: 296. 1912. (*A. bivelatoides* Murrill., Mycologia 4: 297. 1912. *A. Hillii* Murrill Mycologia 4: 298. 1912. *A. McMurphyi* Murrill, Mycologia 4: 299. 1912. *A. glaber* Zeller, Mycologia 30: 469. 1938.)

Photographs of this species were published in a previous paper (Smith 1940) under the name of *A. glaber*, and abundant fresh material has been studied. The study of the type specimens has been greatly facilitated by the information thus gained. The species is not a particularly variable one, but does change color markedly from youth to age, and the annulus is variable insofar as the scales on the under side are concerned. The spores of *A. hondensis* (type) measure $5.5-6.5$ (7) \times $3.5-4$ (4.5) μ . The large spores are unusual, the majority measuring $5.5-6 \times 3.5 \mu$. The bulbous stipe and the double edged annulus are typical of the *A. silvaticus* complex. The pileus although now slightly moldy, apparently was smooth when fresh. -

The type of *A. bivelatoides* has spores $5-6 \times 3-3.5 \mu$. The annulus has the typical double edge of the *A. silvaticus* series of species even though it was described as simple by Murrill. The pilei are identical in color and surface characters with young pilei of my own collections identified as *A. glaber*.

In the type of *A. Hillii* part of the stipe is missing. However, the fungus clearly belongs in the same group as *A. silvaticus* and lacks any characters by which to distinguish it from *A. hondensis*. Its spores measure $5-5.5 \times 3-3.5 \mu$, and the pileus is typical of a mature *A. hondensis*. Here again the "simple" annulus as described is best disregarded. Murrill did not see fresh material.

A. McMurphyi was also described from dried material. The type is a fine, large, mature and hence dark-colored specimen. The spores, double-edged annulus and bulbous stipe are all characteristic. The stipe was apparently about 2 cm. in diameter. The spores are $5-6 \times 3-3.5 \mu$. There are no characters by which to distinguish it from *A. hondensis*.

Material of *A. glaber* from Zeller has also been examined. His specimens were collected by Dr. Burlingham under live oaks at Pacific Grove, California, and his description is the first, incidentally, to correctly characterize the annulus. All of these species have very scattered to clustered saccate cheilocystidia that are often difficult to locate because of their sporadic occurrence and because they frequently do not project beyond the basidia.

AGARICUS FLAVITINGENS Murrill, *Mycologia* 4: 298. 1919. Pileus 4–10 cm. broad, broadly convex or with a flattened apex when young, expanding to nearly plane or plane with a decurved margin, nearly always having a broad flat disc in age, surface dry, shaggy-fibrillose over all except the disc and there merely matted-fibrillose, fibrils “chamois” (pale yellow) or a sordid yellow, “clay-color” (sordid yellowish brown) over the center, toward the margin the fibrils becoming arranged into appressed or slightly recurved sordid yellowish scales, white flesh showing between the scales, in age sometimes glabrescent (particularly after heavy rains) and then the entire surface more or less sordid pinkish; flesh white but quickly changing to “vinaceous pink” when cut or bruised, odor none, taste slightly nutty; lamellae “vinaceous pink” at first, becoming “Japan-rose” and finally dark sordid purplish brown, close but not crowded, almost reaching the stipe, broadest near the margin of the cap (5–7 mm.) and hence rather narrow, edges even but flocculose under a lens from cheilocystidia; stipe 4–7 cm. long, 8–12 mm. thick at apex, stuffed with a silky pith, becoming hollow, base enlarged somewhat or clavate and up to 2 cm. thick, densely white-fibrillose below the superior ring, often with fibrillose zones or patches, glabrescent, glabrous and silky above the ring, becoming sordid pink over all in age; annulus thin, submembranous to almost fibrillose, with inconspicuous yellow patches on under side in some (appearing single in many with the under side merely coarsely fibrillose with white or yellowish fibrils), glabrous and pallid on upper surface.

Spores $4-5 \times 3.5-4 \mu$, subglobose to ellipsoid, dark fuscous in mass and under the microscope; cheilocystidia abundant, cylindric to saccate, $18-32 \times 9-15 \mu$, thin-walled and readily collapsing.

Gregarious to subcespitose on sandy rocky soil under maple, alder, western red cedar and Douglas fir, Baker Lake, Wash., Sept. 5, 1941, *E. B. Mains & A. H. Smith* 16244.

Observations: The type of *A. flavitingens* could not be located but a water-color painting was found. It shows a fungus essentially like the above material. The yellow, fibrillose scales of the pileus and the darker brown disc, stature, and small spores appear to be distinctive of Murrill's species. Murrill described the gill color as avellaneous to umbrinous, the stipe as ochraceous tinted over the lower portion, and made no mention of a color change when the flesh was bruised. Although he described *A. flavitingens* as gregarious, his description reads as though he had drawn it from a single carpophore, and so it is very probable that no idea of the variation of the species is contained in his description. The discrepancies pointed out above should receive some consideration. The change in color when bruised, the difference in the color of the gills of young specimens, and lack of yellow tints in the stipe in age if clearly established might be significant. However, in this instance, when the inaccuracies of Murrill's descriptions are considered on the one hand, and on the other the variation established for some species of *Agaricus* such as *A. placomyces*, it appears best to disregard them at least for the time being. *A. flavitingens* appears to be closely related to *A. Kauffmani* but differs in having a fibrillose sheath below the annulus. Since

this becomes worn away in age, Murrill's description of the stipe as smooth is not a serious discrepancy in view of the fact that he probably based his description on an old specimen. In drying, the stipes of the Baker Lake collection became yellowish. Consequently this change could also be expected on old individuals which were still in the fresh condition.

THE GENUS COLLYBIA

Two previously undescribed species are included here as well as critical accounts of two that needed clarification as far as our North American flora is concerned. No attempt has been made to treat the gray, more or less hygrophanous species now placed in the genus *Lyophyllum*, although several in this group are very abundant in the western United States.

Collybia bakerensis A. H. Smith, sp. nov. Pileus convexus, glaber, pallidus vel incarnato-tinctus; lamellae angustae, confertae, breve decurrentes, albae, saepe vinaceo-tinctae, demum flavo-maculatae; stipes crassus, aequalis, cavus, sursum albidus, deorsum subvinaceus, fibrillosus dein glaber; sporae $4.5-5.5 \times 3-3.5 \mu$.

Pileus 2-4 cm. broad, broadly convex to obtuse when young, the margin curved in against the gills at first, expanded in age and then with or without a low umbo, in some the disc plane and the margin elevated, surface glabrous and moist, appearing appressed fibrillose under a lens in faded condition, sordid watery white when moist and some with a faint flush of incarnate, subshining when faded, opaque at all times; flesh 3-4 mm. thick over the disc and tapering gradually to the margin, watery white, odor and taste mild; lamellae very narrow (1-1.5 mm.), very crowded (58-65 reach the stipe, 4-5 tiers of lamellulae), short-decurrent to broadly adnate, white or with a faint vinaceous flush, occasionally stained sordid yellowish where bruised, edges slightly eroded; stipe short and curved, 1-3 (4) cm. long, (2) 3-5 mm. thick, equal or slightly enlarged at the base, hollow, very pliant, white above, sordid pale vinaceous brown near the base, at first covered by a thin coating of white appressed fibrils, glabrescent, inserted onto the substratum.

Spores $4.5-5.5 \times 3-3.5 \mu$, hyaline, smooth, broadly ellipsoid, not amyloid; basidia four-spored, $18-22 \times 6-7 \mu$; pleurocystidia not differentiated; cheilocystidia fasciculate to scattered, $24-36 \times 6-10 \mu$, clavate, saccate or subcylindric, thin-walled and somewhat contorted or branched in age, hyaline and readily collapsing; gill trama subparallel, the subhymenium thin and ramose; pileus trama homogeneous, the surface hyphae more or less radially arranged and more compact than in the remainder, clamp connections abundant.

Singly on a conifer log, Anderson Creek, Baker National Forest, Wash., Aug. 19, 1941 (A. H. Smith 16278, TYPE).

Observations: When more is known of this species it may be found to be referable to *Collybia xylophila* as a variety. However it appears to differ markedly in both habitat and stature. Taken together these differences appear to be significant, and in view of the lack of information on the microscopic characters of *C. xylophila* it appears best to name the Anderson Creek

collection. The broad cheilocystidia and yellowish stains on the gills indicate that the collection is not just a depauperate form of *C. maculata* even though it is obviously closely related.

Collybia subsulcatipes A. H. Smith, sp. nov. Pileus subconicus demum planus, umbrino-vinaceus demum pallide vinaceus; odor aromaticus, graveolens; sapor mitis; lamellae confertae vel subdistantes (46–54 adnatae), latae, pallide griseo-vinaceae, crassiusculae; stipes crassus, deorsum attenuatus, radicatus, sursum pallide vinaceus, deorsum umbrino-vinaceus; sporae globosae, 5–5.5 × 4.5–5 μ .

Pileus 5.5–8 cm. broad, obtuse with an inrolled margin, becoming gibbous or plane, in age the margin recurved or elevated and frequently splitting, surface moist and polished, margin translucent striate, hygrophanous and opaque when faded, when young "army-brown" to "vinaceous fawn" over all, disc becoming "russet-vinaceous" and margin "deep brownish vinaceous" (dark to pale vinaceous brown), fading to a "pale vinaceous buff" (pallid vinaceous); flesh thin (2–3 mm.), equal, firm and cartilaginous, concolorous with surface of pileus, odor faint but heavy and aromatic (somewhat like that of benzaldehyde) very distinctive; taste mild; lamellae close to nearly subdistant, 46–54 reach the stipe, 1–3 tiers of lamellulae, the lamellulae quite irregular in arrangement, broad (1 cm. \pm), becoming slightly ventricose, depressed adnate to nearly free, color "pale grayish vinaceous" becoming "light russet-vinaceous" (gray with a tinge of vinaceous when young, becoming distinctly dull vinaceous in age), faces glaucous, edges thickish and even; stipe 6–10 (15) cm. long, 10–16 mm. thick at apex, tapered downward to a long pseudorhiza, solid and fibrous within, apex more or less concolorous with the pileus, becoming very dark sordid vinaceous brown from the base upward in age, surface pruinose but soon polished, smooth or longitudinally grooved to subsulate.

Spores globose to subglobose, hyaline, 5–5.5 × 4.5–5 μ , smooth, not amyloid; basidia four-spored, 28–34 × 4.5–6 μ long, slender and subclavate, pleuro- and cheilocystidia not differentiated, gill trama parallel to subparallel, the hyphae more or less cylindric; pileus trama with a thin pellicle of radially arranged subgelationous hyphae 3–4 μ in dia., remainder floccose, the hyphae 5–15 μ in dia.

Gregarious on humus, Storm King Mt., Olympic National Park, Wash., Oct. 5, 1941 (*Helen V. & A. H. Smith 17566*, TYPE); same locality again on Oct. 16 (17962).

Observations: This species is closely related to *Collybia fusipes* but distinct because of its globose spores, odor, and vinaceous gills. *C. fusipes* has slender cheilocystidia in contrast to the absence of cheilocystidia in *C. subsulcatipes*, but no great amount of emphasis should be placed on this difference until old material of the latter can be examined. In species with filamentous cheilocystidia, these organs are sometimes slow in elongating. Excellent dried specimens of *C. fusipes* from Marcel Jossierand, Lyon, France, have been compared. The most obvious difference macroscopically is in the color of the lamellae and their spacing. In *C. subsulcatipes* they are closer and more vinaceous. *C. lancipes* Fr. sensu Rea appears, from the

description, to be quite similar. It has pale flesh-color and rather thick gills as well as practically the same type of stipe. However, its spores are described as $6 \times 4 \mu$, no mention is made of a peculiar odor, and the color of the pileus is given as pale reddish brown. *C. oregonensis* has a similar odor but is readily distinguished by its ellipsoid spores, the color of the gills and stipe, and in general appearance. *C. oregonensis* is closely related to *C. maculata*. *C. collybiiformis* (Murrill) Singer has some of the characters of *C. subsulcatipes* but no mention is made of a peculiar odor and the stipe and gills are described as white.

COLLYBIA CYLINDROSPORA Kauff. Pap. Mich. Acad. 5: 126. 1926. Pileus 3–7 cm. broad, plane with a recurved and wavy striatulate margin, often lobed in age, surface glabrous and moist, “clay-color” to “pinkish buff,” fading as if hygrophanous after heavy rain, becoming pallid to nearly “pale ochraceous buff” (yellowish) and retaining this color when dried or else becoming tinged alutaceous, unpolished when faded or dried; flesh thin, pliant, reviving somewhat (1.5–2 mm. thick), equal, concolorous with the surface, odor and taste not distinctive; lamellae subdistant, 28–30 reach the stipe, 3–4 tiers of lamellulae (outer two tiers very short), moderately broad (5 mm. \pm near the stipe and narrowed toward the cap-margin), bluntly adnate or decurrent by a tooth, seceding, “tilleul-buff” (pallid) when young and old, drying concolorous with the pileus or slightly paler, occasionally stained with rusty brown spots, edges even but wavy; stipe 5–7 cm. long, 3–7 mm. thick at the apex, hollow, terete or compressed, very tough and pliant, velvety to unpolished and distinctly longitudinally grooved, dark brownish moist but fading like the pileus and nearly concolorous with it when dried, base strigose and with numerous white rhizomorphs.

Spores $5-6 \times 2.5 \mu$, narrowly ellipsoid, smooth, not amyloid; basidia four-spored, $20-24 \times 3.5-5 \mu$, subclavate; pleurocystidia not differentiated; cheilocystidia scattered to rare, filamentose, $18-30 \times 2.5-3 \mu$, flexuous; gill trama interwoven, nearly hyaline in iodine (basidia brownish), subhymenium thin; pileus trama homogeneous, the surface hyphae compactly interwoven and slightly narrow than the remainder.

Gregarious to scattered under alder, Park Creek, Mt. Baker, Wash., Sept. 10, 1941 (16811); Baker Lake, Wash., Sept. 13 (16936); Chimacum, Wash. (Olympic Peninsula), Oct. 13, 1941 (17856).

Observations: *C. cylindrospora* is closely related to *C. confluens* and *C. hariolorum*, but is readily distinguished by its sulcate striate or channeled stipe and broad subdistant gills. Among Kauffman's collections two of this species were found. One, the type, and a second identified as *C. proliza* Fr.—Ricken. Apparently this second collection is the basis for Kauffman's report of *C. proliza* from Mt. Hood. The only other collection of *C. proliza* located was an earlier collection which he made at Lake Cushman, Washington, in 1915. This one is much closer to the European concept and is the same species Murrill described as *C. badiialba*. For an account of the latter see Smith (1941). Regardless of whether or not *C. proliza* and *C. badiialba* are synonymous, the report of the former from Mt. Hood cannot

be recognized. Although Kauffman compared his new species with *C. fusipes*, *C. lancipes*, and *C. distorta*, actually there is little or no resemblance to them. *C. cylindrospora* is a *Marasmius*-like fungus with the relationships pointed out above. An examination of Kauffman's type shows that the stipes were unpolished to velvety or at the most glabrous above only. The spacing of the gills appears to be variable, but in all the dried material studied they were most accurately characterized as subdistant. My description was drawn from the material cited above, and is given to supplement that of Kauffman.

The dominant color of the pileus is whitish-alutaceous to yellowish and when properly dried whitish buff with an unpolished appearance. Young or water-soaked specimens have the dark colors given in the description. In general the colors appear to be similar to and to vary much the same as those of *Marasmius oreades* (whitish to rather dark alutaceous), and do not appear taxonomically significant within these limits. The broad subdistant gills and the channelled velvety to unpolished dark colored stipe are the important characters aside from the spores.

More than likely *C. cylindrospora* is a synonym of *Collybia laxipes* (Fr.) Quél., but more information on the microscopic characters of the latter is needed to be certain. Rea (1922) gives the spores of the latter as $5-6 \times 3 \mu$ and elliptical. This may indicate a difference in shape. Rea's description of *C. laxipes* covers the diagnostic features of *C. cylindrospora* remarkably well, and his account is closely in line with the Friesian concept. Quélet's (1873) illustration, however, depicts very small atypical individuals if they are to be judged on the basis of the descriptions of most authors and the Washington and Oregon collections here placed in *C. cylindrospora*.

COLLYBIA EXTUBERANS (Fries) Quélet, Champ. Jura & Vosges, 97. 1872. Pileus 2-5 cm. broad, conic with an inrolled margin when young, becoming broadly conic-campanulate or plane with a low or prominent conic umbo, glabrous, surface viscid when wet but soon dry and very finely radially wrinkled, the margin very thin and soon recurved, sometimes becoming faintly translucent-striatulate, color "bone-brown" (very dark brown with a tinge of red) over all when young, gradually becoming a dull shade of "pecan-brown" or a paler vinaceous brown (but not as red as in *C. badi-alba*); flesh thin, pliant and moderately tough, very sordid reddish brown near the pellicle, paler below, gradually becoming pallid throughout, odor none, taste mild; lamellae close to crowded, 48-56 reach the stipe, 2-3 tiers of lamellulae, distinct, sinuate and attached only by a tooth, narrow to moderately broad (3-5 mm.) equal or narrowed from the stipe to the margin of the cap, "pale pinkish buff" or with a more vinaceous cast (pallid buff to pinkish buff), becoming spotted with very sordid brownish spots, edges only slightly eroded; stipe 4-7 cm. long, 3-6 mm. thick above, more or less tapered at the base to a pseudorhiza-like prolongation which ends in one or more rhizomorphs, longitudinally striate, glabrous, pallid (concolorous with young gills) above, becoming sordid brownish progressively downward (base almost concolorous with the pileus in age).

Spores hyaline, $4.5-6 \times 3-3.5 \mu$, narrowly ellipsoid, smooth, not or only very weakly amyloid (reaction not conclusive); basidia four-spored, $18-26 \times 5-6.5 \mu$, clavate; pleurocystidia and cheilocystidia not differentiated; gill trama of more or less parallel cylindric hyphae $8-15 \mu$ in dia., subhymenium very thin and ramose; pileus trama with a pellicle of radially arranged smooth-walled hyphae $3-4 \mu$ in dia., the layer 2-3 hyphae thick, beneath this a layer of interwoven subgelatinous hyphae with clamp connections, the hyphae $3-5 \mu$ in dia. and the layer $15-30 \mu$ thick, the remainder of the flesh floccose, the hyphae $5-15 \mu$ in dia., the pigment dissolved in the cell sap and most abundant just below the subgelatinous layer.

Cespitose to gregarious on rotten conifer logs, Lake Angeles, Olympic Mts., Wash., Sept. 19, 1941 (16967); Mt. Angeles, Sept. 28 (17368); Olympic Hot Springs, Olympic National Park, Oct. 11, 1941 (17800).

Observations: This species is closely related to *Collybia badiialba* Murrill, but differs distinctly in the shape of its spores, in the organization of the pellicle of the pileus, and in the duller colors as well as in the less crowded gills and radicating stipe. It is also more inclined to be cespitose, but this appears to be a variable character. *C. extuberans* belongs to the same series of species as *C. fusipes*. It apparently differs from the latter in habitat, close, narrower lamellae and more than likely in the organization of the pileus. Cooke's illustration cited for *C. extuberans* by Rea does not depict the species satisfactorily. The stipe, as shown by Cooke, does not taper to rootlike projection and the umbonate character of the pileus is not sufficiently emphasized. Rea's description, however, appears to apply very well and that of Ricken is about equally good. Neither mention the reddish stains which develop on the gills. However, this character appears to be common to most of the radicating *Collybiae* of this series so I would hesitate to use its presence here as a character of any significance, particularly when *C. extuberans* is not too well known.

THE GENUS CLITOCYBE

Although one of the more uninteresting genera of the agarics, the species of *Clitocybe*, both by the abundance of fruiting bodies produced and the large number of species present in our flora, make continued demands on the time of the agaric specialist. They are a rather difficult group because of the general lack of distinctive microscopic characters and intergradation of the macroscopic characters by which species are usually distinguished. In the following account I have brought together the information accumulated on the more unusual species of this genus during the past eight years. Seven species are described as new and accounts of two others which were incompletely or erroneously described are included.

Clitocybe flavissima A. H. Smith, sp. nov. Pileus convexus demum late convexus, siccus, fibrillosus, laete luteus; sapor subpiperatus; lamellae subdistantes, latae, late adnatae, laete luteae; stipes aequalis, luteus, fibrillosus; sporae globosae vel subglobosae, $7-9 \mu$; cheilocystidia $40-200 \times 3-5 \mu$; ad truncos coniferarum, solitarius vel caespitosus.

Pileus 3–5 cm. broad, convex, becoming broadly convex, surface dry and innately fibrillose or moist beneath the fibrils, either remaining fibrillose or becoming more or less scaly around the disc, the fibrils near the margin sometimes arranged into fascicles and the margin usually fimbriate when young, evenly yellow over all ("mustard-yellow") or the disc darker and near "antimony-yellow"; flesh thin but nearly equal (1.5–2 mm.), pliant, dull yellow, odor faintly fragrant, taste slightly peppery; lamellae nearly subdistant, 24–30 reach the stipe, 2 tiers of lamellulae, moderately broad (5 mm. \pm), bluntly adnate but becoming more or less decurrent, bright yellow ("primuline-yellow") becoming "light orange-yellow," edges a brighter yellow than the faces and appearing gelatinous under a lens; stipe 2–5 cm. long, 3–6 mm. thick, equal, hollow, fleshy, concolorous with the pileus in age, pallid when young from the thin pale yellowish partial veil, in age appressed fibrillose to the apex.

Spores globose to subglobose, 7–9 μ , smooth, not amyloid; basidia four-spored; pleurocystidia none, cheilocystidia very abundant, 40–200 \times 3–5 μ , septate, filamentose, subgelatinous, yellowish to hyaline when fresh, the pigment intracellular; gill trama homogeneous, the cuticle of radially arranged hyphae with thickened walls and abundant clamp connections.

Scattered to subcespitose on dead conifer stubs, Ermine Creek, Baker National Forest, Wash., Sept. 11, 1941 (16837, 16928); Mt. Angeles, Olympic Mountains, Wash., Sept. 21, 1941 (17084, TYPE).

Observations: *C. flavissima* is very closely related to *C. decora* but is readily distinguished by its globose spores, long filamentose cheilocystidia and lack of brownish scales on the pileus. These two, *Tricholoma rutilans*, *T. flavescens* and *Pleurotus sulfureoides* form a very natural group or stirps and make up the nucleus of the genus *Tricholomopsis* Singer. In a recent article Singer (1942) added *Tricholoma radiculatum* Pk. and *T. secedifolia* Murrill to *Tricholomopsis*. *Collybia platyphylla* was previously placed here. I have not studied the types of *T. flavescens*, *P. sulfureoides*, or *Clitocybe sulphurea* Pk., but from other material believe that all are identical. The long filamentose subgelatinous cheilocystidia readily distinguish *C. flavissima* from all the species of the *Tricholomopsis* series.

Clitocybe glutiniceps A. H. Smith, sp. nov. Pileus late convexus denum planus (non depressus), viscidus, glaber, striatus, sordide cremeus; lamellae confertae, latae, arcuatae vel brevissime decurrentes, pallide sordido-cremeae; stipes elasticus, canescens, pallidus; sporae 4.5–5 \times 3–3.5 μ .

Pileus 2.5–4 (6) cm. broad, broadly convex with an inrolled margin when young, becoming nearly plane (the disc not depressed), surface glabrous and viscid to the touch, the pellicle somewhat separable, translucent striate on the margin, color evenly pale dirty cream color or in age the disc tinged sordid brown; flesh thin, pliant, concolorous with surface, odor none, taste mild, no color change when bruised or cut; lamellae moderately close, 28–33 reach the stipe, 2 tiers of lamellulae, broadest (2–3 mm.) at attachment, arcuate-adnate to short decurrent, seceding, pale sordid cream color (paler than the pileus), edges even; stipe short, 3–4 cm. long, 4–6 mm. thick at the apex, hollow, rather tough and pliant, whitish from a coating of appressed fibrils which extends to the apex, base sparsely white strigose.

Spores $4.5-5 \times 3-3.5 \mu$, ellipsoid, smooth, not or only very weakly amyloid (reaction doubtful); basidia four-spored; pleurocystidia and cheilocystidia not differentiated; gill trama of narrow interwoven non-amyloid hyphae, subhymenium subgelatinous (in KOH) when revived; pileus trama floccose beneath a somewhat gelatinous pellicle of interwoven hyphae $2-4 \mu$ in dia., hyphae of the flesh $6-15 \mu$ in dia.

Gregarious under conifers, Olympic Hot Springs, Olympic Mountains, Wash., Oct. 2, 1941 (17524, TYPE).

Observations: Although this collection was made under very adverse weather conditions, the carpophores were in good condition and the viscosity of the pileus cannot be disregarded. The pellicle is made up of very narrow hyphae in contrast to those forming the flesh, and exhibits the characters of a truly viscid layer rather than the false viscosity often encountered on various species such as *Inocybe geophylla* in this region.

Because of the somewhat cartilaginous character of the stipe some might be inclined to place the species in *Omphalia*. It is described in *Clitocybe* because of its relationship to *C. brumalis*. Lange's (1935) concept of the latter is very close, but there appears to be a distinct difference in shape of the pileus and the nature of its surface. *C. obsoleta* is also close but apparently differs in having an anise-like odor, in not possessing a viscid pellicle and in the margin of the pileus not being translucent-striate. Lange gives the spores of the latter as $6 \times 3-3.5 \mu$, Rea as $7 \times 4-5 \mu$, and Ricken as $6-7 \times 3-4 \mu$. These measurements are consistently longer than those of *C. glutiniceps*, and indicate an appreciable difference in shape, i.e., ellipsoid contrasted to subglobose.

Clitocybe gomphidioides A. H. Smith, sp. nov. Pileus convexus mox subplanus vel subdepressus, viscidus, glaber, vel minute areolatus, subferruginus; sapor valde farinaceus; lamellae subdistantes vel confertae, crassae, venosae, pallidae mox sordide avellaneae; stipes solidus, pallidus vel sordide avellaneus; sporae (7) $8-10$ (11) $\times 4-5.5 \mu$.

Pileus (3) 5-9 cm. broad, at first plane with an inrolled margin or very slightly arched, expanding to very broadly convex with a depressed disc or plane, in age the margin often elevated and disc broadly depressed, not truly infundibuliform, surface viscid, glabrous or with minute areolate or spotlike scales over the central portion, margin minutely tomentose, color "Mikado brown" on the disc but "orange-cinnamon," "pinkish cinnamon" or "light pinkish cinnamon" toward the margin (color reddish cinnamon on disc, paler cinnamon to ferruginous-cinnamon toward the margin), in age fading to "saya brown" on disc, (duller and more yellowish cinnamon), the margin remaining "pinkish cinnamon," sometimes dull tan with scarcely a trace of red in age, regaining the reddish cinnamon colors when dried; flesh thick and tapered abruptly to the margin, pale "vinaceous buff" and watery punctate, odor and taste very strongly rancid-farinaceous; lamellae subdistant to close, 50-58 reach the stipe, 2 tiers lamellulae, many forked either near the stipe or part way to margin, narrow to moderately broad (3-5-8 mm.), tapered each way, short decurrent, often thickish, intervenose

or wrinkled, near "light pinkish cinnamon" young, "avellaneous" to "wood brown" in age (dark avellaneous); stipe 3-7 cm. long, 9-15 mm. thick, solid, "pale vinaceous buff" within or darker in the base, surface paler than the gills and with a thin coating of pallid appressed fibrils, glabrescent and darker in age, when dry more or less concolorous with the pileus.

Spores (7) 8-10 (11) \times 4-4.5 μ , narrowly ellipsoid to subfusoid, not amyloid, smooth, white in mass; basidia four-spored; pleurocystidia and cheilocystidia not differentiated; gill trama not amyloid; pileus trama with the pellicle made up of an interwoven mass of narrow hyphae with subgelatinous walls, the hyphae 3-5 μ in dia. and not appreciably thinner than those of the flesh, clamp connections abundant.

Gregarious under Devil's club on wet soil, Olympic Hot Springs, Olympic National Park, Washington, Oct. 2 (17504) and Oct. 10, 1941 (17682, TYPE), also at Lake Mills near Wolf Creek, Oct. 12, 1941.

Observations: The outstanding characters of this species are the reddish cinnamon color, viscid cap, gills which change color in aging, long rather narrow smooth spores and very pronounced odor and taste. *Clitocybe incilis* and *C. opiaria* appear to be the most closely related species. The former is not described as viscid and is generally said to lack a farinaceous odor and taste. The illustration by Nuesch (1931) is very suggestive of *C. gomphidioides*, however. Since Fries placed *C. incilis* next to *C. sinopicus* and described the pileus as "non udus" it hardly appears justifiable to place a viscid species under the Friesian name. *C. opiaria* also differs in not having a viscid pileus, and its gills are not described as becoming dark avellaneous. The odor and taste are also different according to descriptions.

In the Olympics, where various species of *Gomphidius* are very abundant, one could easily pass by this *Clitocybe* thinking it was just an abnormal growth of a reddish *Gomphidius*. The thick, veined, forked, dark-colored gills at maturity, the stature of the carpophore, and the color of the pileus all contribute to this impression. The spores also remind one of the spores of a *Gomphidius* because of their subfusoid shape. However, they are white in mass and since other members of *Clitocybe* have similarly shaped spores, the resemblance does not appear significant.

Clitocybe michiganensis A. H. Smith, sp. nov. Pileus late convexus vel subplanus, cinereo-canescens demum politus, hygrophanus, olivaceo-fuliginosus mox pallidus; lamellae confertae, adnatae vel subdecurrentes, olivaceo-fuligineae; stipes aequalis, cavus, cinereo-canescens demum glaber et fuliginosus; sporae 4-4.5 \times 2.5 μ .

Pileus 1-2.5 cm. broad, very broadly convex to nearly plane and with an inrolled margin at first, becoming broadly convex to plane in age, surface appearing dry at first from a hoary-canescient thin coating of fine gray fibrils, glabrescent and then moist and polished, when covered with fibrils appearing pale glaucous gray, when polished evenly "hair-brown" to "drab" (nearly putty color); hygrophanous and fading to pale gray or whitish, usually fading on disc first; flesh thin, equal, concolor with surface, watery, taste strongly rancid-farinaceous, odor faintly so; lamellae close to almost crowded, 30-40

reach the stipe, 2 tiers of lamellulae, adnate at first, short-decurrent at maturity, narrow, nearly equal, "drab" or with an olivaceous tinge when young, sometimes paler and more sordid in age; stipe 2-3 cm. long, 2.5-5 mm. thick equal or slightly enlarged below, hollow, grayish within, surface covered like the pileus with a thin coating of glaucous fibrils, glabrescent and then concolorous with the naked cap.

Spores $4-4.5 \times 2.5 \mu$, narrowly ellipsoid, not amyloid, smooth, basidia four-spored; pleuro- and cheilocystidia not differentiated; gill trama not amyloid, of moderately broad hyphae; pileus trama homogeneous, not amyloid, clamp connections present.

Scattered or solitary on debris in oak woods, Oct. 30, 1940, Ann Arbor, Mich. (15505, TYPE).

Observations: When the canescent fibrillose covering of the cap and stipe have been worn away, this species is similar in color to *C. ditopoda*. It differs from the latter in its narrowly ellipsoid spores, pronounced canescent fibrillose coating over pileus and stipe when young, strongly rancid-farinaceous taste, and the much smaller size. In addition, *C. michiganensis* appears to fruit in a solitary or widely scattered manner rather than being densely gregarious as in *C. ditopoda*. *C. mortuosa* sensu Ricken differs in having paler gills and a glabrous pileus. *C. vilescens* Pk. is almost identical in appearance with *C. michiganensis* but can be distinguished by its taste and microscopically by its spores.

During the season 1937 *C. vilescens* was collected in a pasture in southern Oregon. The specimens were fruiting on the accumulated debris around an old oak stub, Kirby, Oregon, Nov. 26, 1937 (9092). The spores measure $5-6 \times 4-4.5 \mu$, are smooth, broadly ellipsoid to subglobose, and not amyloid. The basidia are four-spored, no cystidia are differentiated, the gill trama is composed of narrow hyphae, and the pileus trama has a cuticle of interwoven hyphae $2-4 \mu$ thick, the hyphae of the trama itself are $5-10 \mu$ thick. Clamp connections are present. The macroscopic characters are as Kauffman (1918) gave them except that the margin of the pileus may be faintly striatulate in age when wet, and the gills may be rather dark cinereous.

Clitocybe piperata A. H. Smith, sp. nov. Pileus convexus vel late convexus, pruinosis et pallidus, mox politus et alutaceus; sapor valde acris; lamellae confertae vel subdistantes, adnatae vel subdecurrentes, angustae, pallidae demum olivaceo-cinereae; stipes clavatus, solidus, impolitus, sursum pruinosis, pallidus; sporae $4-5.5 (6) \times 2-2.5 \mu$.

Pileus 6-12 cm. broad, convex to obtuse and with an inrolled margin when young, in age broadly convex to plane or the margin wavy and uplifted slightly, regular or occasionally either sinuate or lobed, surface at first moist beneath a hoary pruinose covering caused by fine projecting microscopic hairs $20-42 \times 3-4 \mu$, becoming glabrous and occasionally with watery spots around the disc, opaque, color pallid at first ("tilleul-buff"), or very pale avellaneous with a chalky white sheen, gradually becoming dull yellowish brown ("clay-color") when still moist, fading as if hygrophanous (in old caps) to "light buff" (dull yellowish), when dried varying between

pale buff and alutaceous; flesh thick (about 1 cm. on the disc), tapering evenly to the margin, pallid to pale buff, somewhat punky in texture, odor faintly fragrant in young caps, becoming somewhat disagreeable at maturity, taste very sharply acrid (as in *Russula emetica*) and sometimes with a bitter after taste, no color change when cut or bruised. Lamellae nearly crowded in small caps, almost subdistant in large ones, rounded or bluntly adnate and becoming sinuate with a short decurrent tooth or becoming merely short-decurrent, narrow to moderately broad (5 mm. \pm), "tilleul-buff" (pallid) at first, gradually becoming darker, pale olive-buff to subavellaneous ("olive-buff" to "pale olive-buff") or in age fairly dark avellaneous, "pinkish buff" (yellowish) in dried specimens, edges even to eroded and thickish in some specimens; stipe 4–9 cm. long, 1–2 cm. thick at the apex, clavate, 2–3 cm. at base, solid, usually somewhat pointed below the enlarged portion, rather tough to punky and firm in texture, pallid to pale buff within, surface unpolished at first, more or less pruinose toward the apex, base slightly cottony and with a few rhizomorphs, glabrous but somewhat scaly in age from the torn cuticle.

Spores 4–5.5 (6) \times 2–2.5 μ , subcylindric to subfusiform, smooth, (a few appearing very slightly wrinkled under an oil immersion lens), not amyloid; basidia four-spored; pleuro- and cheilocystidia not differentiated; gill trama subparallel, the hyphae with long and moderately wide (5–8 μ) cells, not amyloid; pileus trama floccose beneath a thick cuticle of compactly interwoven hyphae 4–8 μ in dia. which give rise to numerous projecting hairs 3–4 μ thick, not amyloid and the walls not truly gelatinous in KOH, clamp connections rare.

Gregarious around or on old stumps and logs in low hardwood forests, Pontiac, Mich., Aug. 24, 1937 (7212); Kent Lake, Oakland County, Mich., Sept. 24, 1940 (15462, type); same locality, July 31, 1942 (18540); Dexter, Mich., Aug. 14, 1942 (18671) and Aug. 17 (18735).

Observations: The outstanding features of this species are the small narrow spores, acrid taste, olive-buff gills in age, and the progressive color change of the pileus as it matures. *C. piperata* appears to be related to *C. innornata* by its gill characters (both attachment and color), its spores, and by the broadly convex to plane pileus. The spores vary in shape from almost truly cylindric to somewhat sway-backed or ventricose and hence are subfusoid. Such small narrow spores as this are known for several different species in *Tricholoma* and *Clitocybe*, but in no species of either genus have I found the combination of characters listed above.

Clitocybe sublutea A. H. Smith, sp. nov. Pileus convexus dein late depressus, glaber subviscidus, striatus, hygrophanus, pallide luteo-alutaceus demum pallidus; lamellae subdistantes, decurrentes, latae, pallide sulphureae; stipes aequalis, glaber, sursum pallide sulphureus, deorsum subalutaceus; sporae 4.5–5.5 \times 3.5 μ .

Pileus 2.5–5 cm. broad, broadly convex with an incurved margin when young, in age the margin uplifted and the disc broadly depressed, glabrous and slightly viscid when moist, margin translucent-striate, color "cartridge-buff" over all when young (very pale yellowish), in age darker on the disc and near "pinkish buff" (buff), hygrophanous, pallid when faded; flesh

thick on the disc (4–6 mm. near the stipe), tapering rapidly to margin, concolorous with cap in either moist or faded condition, not changing when bruised, odor and taste not distinctive; lamellae subdistant, 2–4 tiers of lamellulae, long- and unequally-decurrent, broad (5–7 mm.), tapered each way, color “ivory yellow” (pale yellow) both in young and old specimens, not changing when bruised, edges wavy; stipe 5–7 cm. long, 4–7 mm. thick, usually somewhat eccentric or the cap aborted on one side, hollow, equal or narrowed downward, glabrous above, concolorous with the gills near apex, darker downward, cinnamon-buff at the base in age, base sparsely white strigose.

Spores $4.5\text{--}5.5 \times 3.5 \mu$, ellipsoid, smooth, not amyloid; basidia four-spored; pleuro- and cheilocystidia not differentiated; gill trama somewhat interwoven, not amyloid, the hyphae narrow; pileus trama homogeneous, the hyphae on the surface the same size or slightly smaller than the others and distinctly gelatinous, clamp connections abundant.

Gregarious under alder, Port Angeles, Wash., Oct. 13, 1941 (17830, TYPE).

Observations: The pale yellowish colors, subdistant gills, very small ellipsoid spores, and lack of a farinaceous or bitter taste distinguish this species. I hesitate to place much emphasis on the viscidility of the pileus because the pilei had been subjected to steady rain during most of their development. The species appears to be most closely related to *C. subinversa*, but the spores definitely distinguish it. It differs, apparently, from *C. obsoleta* in its yellowish subdistant gills as well as in the more pronounced yellowish color of both cap and stipe. From *C. subalutacea* sensu Ricken it differs in having an hygrophanous pileus and larger ellipsoid spores. In stature *C. sublutea* bears a striking similarity to *C. ectypa* sensu Lange and other recent European authors. However, it differs in the lack of fuscous fibrils over the disc and in having smaller spores. *C. hypnorum* (Brond.) Rea is very similar in many respects but is said not to be hygrophanous and to have “somewhat crowded” gills. The American species should also differ in having a striate, subviscid pileus. *C. isabella* Quélet is also a somewhat similarly colored species, but from available information does not appear to be identical.

Clitocybe virgata A. H. Smith, sp. nov. Pileus convexus vel planus, sinuosus, siccus, fibrillosus demum subsquamulosus, disco cinereo-fuscus, ad marginem pallidus; lamellae angustae, confertae, adnatae vel brevissime decurrentes, albae demum cremeae; stipes clavatus, deorsum 3 cm. crassus, solidus, albidus, sursum subpruinosis, deorsum impolitus, glaber; sporae $5\text{--}6 \mu$, globosae.

Pileus 5–14 cm. broad, broadly convex or flattened and the margin de-curved at first, more or less expanded to plane in age or margin undulating or wavy and more or less uplifted, often sinuate or irregular, surface appressed fibrillose, dry, color dirty grayish brown over the center and streaked grayish on a pallid ground color toward the margin, in age becoming minutely fibrillose-scurfy, margin pallid to sordid buff; flesh thick, firm, dry, white, unchanging or slowly pale buff where bruised or cut, odor and

taste not distinctive; lamellae narrow (5–6 mm.), close, adnate when young but short decurrent at maturity, many tiers of lamellulae, whitish but becoming cream-colored in age or stained brownish where damaged by insects, intervenose in small caps, edges even or eroded; stipe 5–10 cm. long, 1–2 cm. thick at apex, up to 3 cm. at base, clavate, solid, white within, surface white and unchanging, fibrillose-pruinose near the apex, glabrous below but dull and unpolished, base white cottony.

Spores globose, 5–6 μ , smooth, not amyloid; basidia four-spored; pleurocystidia and cheilocystidia not differentiated; gill trama subregular, not amyloid; pileus trama not amyloid, homogeneous beneath a compact pellicle of interwoven hyphae about the same size as those of the flesh, clamp connections present but rare.

Gregarious in an oak woods on humus, Oakland County, Mich., Sept. 24, 1940 (15468, TYPE).

Observations: The grayish streaked pileus reminds one of that of *Collybia platyphylla*, but the resemblance is superficial. The closer, short-decurrent gills, globose spores and lack of cheilocystidia distinguish it at once. It appears to be most closely related to *Clitocybe nebularis* from which its spores readily distinguish it. The description of *Clitocybe fumosa* in the North American Flora reads a good deal like the above, but the cap is described as smooth and glabrous. European authors are generally agreed that *Agaricus fumosus* Pers. is a member of the series of forms grouped around *C. aggregata*. These are variously placed in *Tricholoma*, *Clitocybe*, and *Collybia*, and are not truly related to the fungus described here. Most of them probably belong in the modern genus *Lyophyllum*. It is possible that *Tricholoma tenuiceps* Cke. & Masee is identical with *C. virgata*, but with the information available at present this does not seem likely. *T. tenuiceps* may also be a member of the *C. aggregata* complex, and, to judge from the description, its pileus does not become fibrillose-squammulose. Von Höhnelt (1919) transferred *T. tenuiceps* to *Russula* but his study was not based on authentic specimens. Pearson (1935) lists the opinions of Quélet, Maire, and Rea on Cooke's plate 1166. Maire was the only one to suggest a similarity to *Collybia platyphylla*, and he made that questionable. From Cooke's illustration it is apparent that the gill attachment in *T. tenuiceps* is quite different from that of *C. virgata*.

CLITOCYBE ALEXANDRI (Gillet) Konrad, Bull. Soc. Myc. Fr. **43**: 186. 1927.
? *Clitocybe Harperi* Murrill, Mycologia **3**: 190. 1911.

Pileus 6–15 cm. broad, plane with a strongly inrolled margin at first, soon shallowly depressed, in age the margin elevated and frequently lacerated or irregular giving the caps a broadly infundibuliform appearance, the margin long remaining inrolled, surface smooth and glabrous at first but appressed felty-fibrillose if viewed under a lens, disc becoming more or less fibrillose-furfuraceous, typically dry (but when water-soaked appearing subhygrophanous) occasionally mottled with large watery spots, color sordid and near "vinaceous buff" at first, more alutaceous when moist or water-soaked (but

such caps fading to "tilleul-buff," hence pallid), in aging gradually becoming grayish, old caps sometimes sordid drab; flesh thick, ± 15 mm. near the stipe, tapered evenly to the margin, pallid but gradually becoming grayer in age, odor and taste not distinctive; lamellae crowded, narrow (4–5 mm.), 3–4 tiers of lamellulae, adnate but soon becoming decurrent, somewhat intervenose, pallid when young ("tilleul-buff") but gradually cinerescent and in age pale dirty gray to dark sordid brownish, separable, edges even; stipe 5–10 cm. long, 10–30 mm. thick, clavate, solid, pallid within, surface uneven, unpolished to appressed fibrillose, concolorous with pileus and discoloring in the same manner, becoming quite sordid in age.

Spores 4–4.5 \times 3–3.5 μ , smooth, broad, white in mass, not amyloid; basidia four-spored; pleuro- and cheilocystidia none seen; gill trama homogeneous, not amyloid, the hyphae somewhat interwoven; pileus trama homogenous, the cuticle of narrow interwoven hyphae, not amyloid.

Scattered under spruce, Fort Dick, Calif., Nov. 10, 1937 (8602); Crescent City, Calif., Dec. 7, 1937 (9490); under alder and cedar, Port Angeles, Wash., Oct. 13, 1941 (17824).

Observations: This species is not uncommon along the Pacific Coast from Washington to California. It can readily be distinguished from *Clitocybe nebularis* by its changing gills and generally more sordid appearance. In addition its spores are consistently a little smaller. Lange's (1935) illustrations depict our West Coast form more accurately than do those of other authors. Partly developed pilei are likely to be squatty in appearance and to have very thick stipes. This is the stage figured by Konrad and Maublanc (1924–1933). This species, to judge by the few references to it in the literature, is either rare or rarely collected and identified. Since it is so unattractive, it is possible that many collectors have passed it by thinking that the material was too old to study. It apparently has not been reported from North America, but an examination of the descriptions of new species of West Coast *Clitocybeae* published by Murrill reveals that *C. Harperi* is very likely identical. Singer (1942) has reported a study of the type of the latter in which he pointed out that the species is closely related to *C. nebularis*. This in addition to the cinereous gills of *C. Harperi* certainly indicates identity with *C. Alexandri*. However, I have not had an opportunity to compare my specimens with the type. Konrad (1936) has discussed at some length the synonymy of this species, and has pointed out that *Parillus griseo-tomentosus* (Secc.) is very likely identical and that the combination *Clitocybe griseo-tomentosus* (Secc.) Konrad ought to be used if the synonymy is accepted and the rules regarding priority are rigidly adhered to. Like Konrad, I have used the name Gillet gave to the species in order to be consistent with recently established usage and to avoid accepting a name that has long been doubtful and over which there might easily be a difference of opinion in the future.

CLITOCYBE AVELLANEIALBA Murrill, *Mycologia* 5: 207. 1913. Pileus (4) 8–12 (20) cm. broad, when young obtusely umbonate with a flattened mar-

ginal area and an inrolled margin, sometimes more or less convex, becoming plane or slightly depressed, the umbo sometimes obsolete, in age at times broadly infundibuliform, margin minutely grayish-fibrillose-pubescent, surface moist, slightly scabrous in some, cuticle occasionally broken into scales in age, toward the margin somewhat fibrillose-streaked, not truly hygrophane (when water soaked appearing subhygrophane), color "clove-brown" to "mummy-brown" when young and moist (nearly black with very little brown), fading slowly to "drab" and finally dark or pale cinereous to avellaneous, margin ribbed or plicate in some; flesh white, not watery, thin, pliant, odor and taste slightly pungent and subrancid; lamellae narrow (4-5 mm.) nearly equal in width and unequally decurrent on the stipe, close but not crowded, 57-64 decurrent on the stipe, 2 tiers of lamellulae, pallid at first ("tilleul-buff"), in age becoming slightly cream colored but the change often not pronounced, edges even; stipe 6-12 (18) cm. long, 1-3 cm. thick at apex, clavate, up to 4 cm. thick at base in large carpophores, stuffed becoming hollow, cortex thin but tough, surface glabrous and uneven, unpolished at first but in age more or less polished, sometimes with scattered appressed fibrils, concolorous with or paler than the pileus, base with only a thin appressed white mycelium and either abruptly rounded below or drawn out to a point causing the stipe to appear subfusiform.

Spores 8-10 (11) \times 4-5.5 μ , broadly fusiform or somewhat inequilateral, hyaline, smooth, not amyloid; basidia four-spored; pleuro- and cheilocystidia not differentiated; gill trama not amyloid, of interwoven hyphae; pileus trama characterized by a thin pellicle of slightly gelatinous hyphae (in KOH) with dark brown contents, the remainder floccose and hyaline, not amyloid, clamp connections abundant.

Gregarious to subcespitose on humus and rotting wood, under alder or mixed conifers, common. Crescent Beach, Joyce, Wash., Oct. 3, 1935 (2846) and Sept. 24 (2582); Orick, Calif., Dec. 5, 1935 (3790); Trinidad, Calif., Dec. 11, 1935 (3938); Martin Lake Trail, Mt. Baker, Wash., Sept. 8, 1941 (16723); Elwha River, Olympics, Wash., Sept. 27, 1941 (17336); Olympic Hot Springs, Oct. 2 (17538); Mt. Angeles, Oct. 4 (17549), and Storm King Mt., Olympic National Park, Oct. 16, 1941 (17963).

Observations: The identity of this species puzzled me for a long time, but since Singer (1942) corrected Murrill's erroneous statements in regard to the spore size and shape, it becomes apparent that my collections belong here. The species is so abundant in the Puget Sound region that a collector would have difficulty overlooking it. It has a slight superficial resemblance to *Clitocybe atrialba* to which Murrill compared it, but cannot be considered closely related. In its spore characters it resembles *C. inornata* somewhat but after studying abundant fresh material of both species, I have been unable to note any additional resemblance. Macroscopically *C. avellaneialba* reminds one of *C. clavipes*, in fact, the two are quite similar in all except spore characters.

The avellaneous color emphasized by the name was not apparent in my specimens until they were quite well faded and then it was not really char-

acteristic. Dark fuliginous, the other color term used by Murrill, is much more accurate.

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JUNIPERUS VIRGINIANA, J. HORIZONTALIS AND J. SCOPULORUM—I. THE SPECIFIC CHARACTERS¹

NORMAN C. FASSETT

This study is based primarily on the writer's collections and photographs, made in the region from Maine to Montana, and south to Georgia, Arkansas and Colorado, and financed in large part by the Wisconsin Alumni Research Foundation. Much of the material in the Arnold Arboretum, the Gray Herbarium, the New York Botanical Garden, Iowa State College, and the University of Wisconsin has been examined, and friends in Kansas, Oklahoma, Missouri, Texas, and New Mexico have contributed mass collections, most of which will be discussed. Mass collections have been made, consisting of a small twig from each tree in a colony, and representing many more individual trees than are present in any herbaria; these collections have been of particular value in solving problems of variation within a colony as compared to the variation within a species. Data have been taken from each individual and tabulated for the colony; tables 1, 2, 4, and 6 are representative of these tables.

Because of the remarkable variation in most colonies of these species, because a colony may consist of one variable species or of two species growing together, with or without intermediates, and because photographs of individual trees are often essential for an understanding of a colony, the writer feels that he is not competent to hold an opinion concerning species in regions where he has not collected, photographed and studied trees in the field. Therefore, *J. silicicola* (Small) Bailey, from the southern states, and *J. lucayana* Britton, from the West Indies, are not considered here, and the southern limits of *J. virginiana* are left indefinite. Likewise the European *J. Sabina*, which in some of its phases is indistinguishable, in the herbarium, from the American *J. scopulorum*, is omitted from consideration because the writer has not studied it in the field. In fact, *J. Sabina*, as represented in the Arnold Arboretum, may have leaves overlapping or not overlapping, with tips obtuse or acuminate, and even with erose margins, while the peduncles may be mostly straight or up to 88 per cent curved; these are characters which separate species in North America.

Juniperus virginiana, *J. horizontalis* and *J. scopulorum* are distinguished from the other species of North America north of the Gulf States by having opposite, scale-like, entire-margined leaves, and blue fruits.

¹ Publication of the tables was assisted by the Lucien M. Underwood Memorial Fund.

TABLE 1. *Ten individuals of J. virginiana from Quincy, Michigan.*

Width in μ of epidermal cells of leaves							Peduncles			Length in mm. of cones							
5	10	15	20	25	30	Av.	Hooked	Straight	% hooked	4	4.5	5	5.5	6	6.5	7	Av.
8	18	3	1 ^a	9.5
8	16	5	1	9.8
5	17	8	10.5
6	14	10	10.7	0	14	0	3	6	2	4.5
2	20	8	11.0	4	7	36	3	5	2	4.5
4	17	7	2	11.2
2	16	12	11.8	0	6	0	..	1	2	3	5.1
3	13	14	11.8
2	16	10	2	12.0	0	6	0	..	1	5	4.8
1	17	11	1	12.0	1	13	7
41	164	88	7	11.0	5	46	10	6	13	11	3	4.7

^a This line signifies: 8 cells were 5 μ wide, 18 cells were 10 μ wide, 3 cells were 15 μ wide, one cell was 20 μ wide, and the average for that individual tree was 9.5 μ .

There are three facts which have sometimes made the differentiation of these three species difficult.

First, the variation within a species is often more conspicuous than differences between species. Well-known, of course, is the striking difference between the juvenile, acicular type of foliage and the adult, scale-like type. While usually the acicular foliage is produced by the younger trees and the scale-like foliage develops later, individual trees show divergence from

TABLE 2. *Ten individuals of J. virginiana var. crebra from Hopkinton, Massachusetts.*

Width in μ of epidermal cells of leaves							Peduncles			Length in mm. of cones							
5	10	15	20	25	30	Av.	Hooked	Straight	% hooked	3	3.5	4	4.5	5	5.5	6	Av.
4	6	8.0	0	6	0	1	2	2	4.6
3	7	8.5	12	23	8	1	3	7	5	4	5.2
5	3	2	8.5	0	35	0	10	10	4.8
3	4	3	10.0	1	18	5	1	..	5	2	2	4.2
4	2	4	10.0	1	9	10	1	4	2	1	5.1
..	9	1	10.5	1	26	4	..	1	7	9	3	4.4
2	5	3	10.5	3	9	25	3	6	1	4.4
1	6	3	11.0	2	1	2	2	3	1	4.7
1	5	3	1	12.0	1	9	10	1	4	1	5.0
..	5	4	1	13.0	7	21	25	..	2	16	10	4	4.2
23	52	23	2	10.2	16	156	9	1	5	34	46	39	11	6	4.6

TABLE 3. Summary of 15 mass collections from Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Virginia, Georgia, Michigan, Wisconsin, Mississippi, and Arkansas.

Width in μ of epidermal cells of leaves						Peduncles			Length in mm. of cones								
5	10	15	20	25	Av.	Hooked	Straight	% hooked	3	3.5	4	4.5	5	5.5	6	6.5	Av.
277	1111	511	66	1	10.9	36	574	6	7	34	92	139	131	42	13	1	4.6

this system. *J. virginiana* f. *Bermerae* Macbride has only acicular foliage; the type belongs, incidentally, to var. *crebra* Fernald & Griscom, but a similar phenomenon occurs in typical *J. virginiana*, as well as in *J. horizontalis* and in *J. scopulorum*. On some trees twigs with acicular foliage are intermixed with those bearing scale-like foliage, and on others all the foliage is intermediate in form between the two types. Injury, especially by the rust *Gymnosporangium*, may cause local reversion to the acicular foliage.

Other differences may pervade a colony; for example, the proportion of width to breadth of the needles may vary greatly from tree to tree (Am. Jour. Bot. 30: 472. 1943). The variation within any colony is often as great as within the species as a whole; this fact is fundamental to an understanding of the taxonomy of the group. The color of the foliage often shows as much variation within a colony as it does within the species, and the writer has Kodachrome pictures of *J. horizontalis* with a bright green individual

TABLE 4. Ten individuals of *J. horizontalis* from Baileys Harbor, Wisconsin.

Width in μ of epidermal cells of leaves						Peduncles			Length in mm. of cones							
10	15	20	25	30	Av.	Hooked	Straight	% hooked	4.5	5	5.5	6	6.5	7	Av.	
5	19	4	2	15.5	7	0	100	
8	12	9	1	15.5	5	0	100	
2	17	9	2	...	16.8	
8	10	6	5	1	16.8	3	1	75	1	1	2	5.6	
4	11	14	1	17.0	7	0	100	
2	16	9	3	17.2	15	0	100	3	4	1	5.9	
2	14	9	5	17.8	6	1	86	3	1	2	6.4	
3	6	16	5	18.8	4	3	57	1	1	3	5.7	
1	9	13	7	19.3	6	3	67	1	1	1	1	5.8	
1	3	19	6	1	20.5	3	0	100	
36	117	108	37	2	17.5	56	8	87	3	6	12	3	3	5.9	

TABLE 5. *Ten herbarium sheets of J. horizontalis from the Province of Quebec, in the herbarium of the Arnold Arboretum.*

Width in μ of epidermal cells of leaves					Peduncles			Length in mm. of cones							
10	15	20	25	Av.	Hooked	Straight	% hooked	4	4.5	5	5.5	6	6.5	7	Av.
13	11	6	..	13.8
11	15	3	1	14.0
11	13	6	...	14.2
5	22	3	14.7	28	10	74	..	5	13	4	4	...	2	5.3
5	20	5	..	15.3
4	18	7	1	15.8
1	23	6	..	15.8
5	16	6	3	16.1	21	4	84	1	...	13	6	2	5.3
2	16	11	1	16.8
3	14	8	5	17.5
60	168	61	11	15.4	49	14	78	1	5	26	10	6	..	2	5.3

growing next to a glaucous one; they look more different than do many distinct species of *Juniperus*, but glaucous individuals seem to grow throughout the range of the species, in company with the ordinary bright green ones. Similarly striking are the shades of green of *J. virginiana*, varying within a single patch to colors bordering on the browns and purples. Shape of tree, size of fruits, etc., may vary throughout a colony, or in other cases there may be local phases. But most of these forms must be considered only as individual variations.

TABLE 6. *Ten individuals of J. scopulorum from Mammoth Hot Springs, Yellowstone National Park, Wyoming.*

Width in μ of epidermal cells of leaves						Peduncles			Length in mm. of cones							
5	10	15	20	25	Av.	Hooked	Straight	% hooked	4	4.5	5	5.5	6	6.5	7	Av.
...	14	12	2	2	13.7	18	21	46	1	...	1	5	5.2
1	7	12	8	2	15.2	1	6	14	1	4	1	1	6.1
1	6	14	9	..	15.2	9	7	56	1	2	3	...	6.2
...	3	19	8	15.8
...	2	20	8	16.0	23	15	61	1	3	3	1	1	5.9
...	6	14	8	2	16.0
...	5	16	7	2	16.0
1	2	14	13	..	16.5	15	17	47	3	3	7	5.7
...	3	14	12	1	16.8
...	2	15	11	2	17.2	8	17	32	3	4	6	...	1	6.0
3	50	150	88	11	15.8	74	83	47	4	4	11	13	17	5	2	5.6

Second, the specific characters are often fully as variable as any others, but they vary in a different way and show reliable statistical differences. For example, straight peduncles may be found on *J. horizontalis* and hooked ones on *J. virginiana*, but these species may be distinguished by the fact that *J. virginiana* has a third or fewer of its peduncles hooked, while *J. horizontalis* has two-thirds or more of them hooked. Observation of a single peduncle is meaningless; examination of 10 peduncles will usually serve for positive identification. Diagnostic characters in width of epidermal cells of leaves, size of cones, seeds per cone, and in the markings on the seeds, are all of this statistical nature.

Third, two species may occur together in a colony, and hybrid swarms may or may not be formed. Hybrid swarms of *J. virginiana* and *J. horizontalis* occur on the coast of Maine and in the Driftless Area. In central and western South Dakota, and in northwestern Nebraska, the range of *J. virginiana* overlaps with that of *J. scopulorum*, and any colony may show a confusing set of interspecific variations. In the Big Horn Mountains, and about Banff, and probably elsewhere, *J. scopulorum* and *J. horizontalis* both grow, and they present some puzzling recombinations of specific characters, perhaps as a result of hybridization. These areas will, it is hoped, be discussed in subsequent papers.

The following specific characters are valid *except* in those regions, just listed, where two species grow together. Most of the statements below must be understood as having the limitation: *except in regions where two species occur*.

Character 1. The main trunk of *J. virginiana* is always erect, that of *J. horizontalis* is creeping, and that of *J. scopulorum* is erect or divided into several more or less ascending trunks. The rounded crown of *J. scopulorum*, originally used as a specific character,² is not always characteristic. When individual branches of *J. horizontalis* are infected with *Gymnosporangium* they may be erect and bear needles of the acicular type.

Character 2. The epidermal cells of the leaves of *J. virginiana* are from 5–20 μ wide, mostly 10 μ , those of an individual plant averaging 9–12 μ ; in *J. horizontalis* they are 10–30 (rarely 5 or 35) μ wide, mostly 15 μ , averaging 13–19 μ ; in *J. scopulorum* they are 5–25 μ wide, mostly 15 μ , averaging 15–19 μ . These measurements are perhaps the best means of distinguishing *J. virginiana*, in the herbarium, from the other two species. Yet the width of epidermal cells is very variable on each leaf; it is the mode and the mean which are diagnostic. For this reason it is necessary to measure a number of cells on each plant (thirty appears to be sufficient) and find the average. In this study, examination was made with a compound microscope, using a 32-mm. objective giving an enlargement of about 70 times; by means of a

² Sargent, Gard. & For. 10: 420. 1897.

camera lucida the width of each cell was marked on the edge of a sheet of paper, then measured with a scale previously prepared from a micrometer slide with the same microscope and camera lucida. Cells were measured to the nearest 5 μ , grouped in classes of 5, 10, 15, 20, 25, or 30 μ each, and averaged. Results for characteristic colonies are shown in tables 1, 2, 4, and 6, those for a large number of individuals totalling nearly 2000 individual cells in table 3, and for the herbarium material from a single region in table 5. It will be seen that all averages for individual plants show agreement, probably within the variation which might be expected from the relatively small numbers of cells measured per individual; indeed, when three individuals from one clone of *J. horizontalis* were measured they showed about as much variation as do the different plants of a colony. Here the variation within the species is not only equalled by the variation within the colony, but is nearly equalled by the variation within each individual.

Character 3. In *J. virginiana* each leaf nearly always overlaps the leaf directly beyond it; in *J. horizontalis* the leaves usually overlap; in *J. scopulorum* they rarely overlap, so that the exposed portion of each leaf usually appears 4-sided. The amount of overlapping of leaves may vary on any twig, particularly in *J. horizontalis*, where there is sometimes lack of overlap after the fashion of *J. scopulorum*. The principle, stated in the fourth paragraph of this paper, that variation within the colony may equal the variation within the species, may be observed by study of the amount of overlap of leaves on many twigs from one colony, as illustrated in *Am. Jour. Bot.* **30**: 472. 1943; in figure 17 of that paper, for example, some leaves barely overlap while others overlap a considerable distance.

Character 4. The apiculate leaf-tips of *J. horizontalis* are variable in length, but always present. They are occasionally present on the acute to acuminate leaf-tips of *J. virginiana*; a large colony of that species at Janesville, Wisconsin, is exceptional in that the leaves are apiculate on all of the 37 individuals with scale type foliage which were sampled. The leaves of *J. scopulorum* are subacute to very blunt, very exceptionally with tips which might be called subapiculate. The acicular leaves of all three species are pointed in about the same manner.

Character 5. While the foliar glands of *J. virginiana* and *J. horizontalis* rarely attain the size of those of *J. scopulorum*, occasional large individuals preclude the use of length as a diagnostic character. But the length of the gland of *J. scopulorum* equals or usually exceeds the distance from the gland to the tip of the adult type of leaf, while in the other two species the gland is always much shorter than that distance.

Character 6. Some of the manuals describe *J. virginiana* as having cones on straight peduncles, and *J. horizontalis* as having hooked or recurved peduncles. As a matter of fact, both straight peduncles and recurved

peduncles may be found on all three species, but the proportions of each are diagnostic. In *J. virginiana* the peduncles are all straight or up to 33 per cent curved; in *J. horizontalis* they are 60–100 per cent curved; in *J. scopulorum* they are 8–70 per cent curved. This character, it may be observed, will always serve to differentiate fruiting specimens of *J. virginiana* and *J. horizontalis*, and will sometimes serve to distinguish *J. scopulorum* from one of the other two species.

Character 7. *J. scopulorum* generally takes two years for fruit to mature, *J. virginiana* but one year; this was originally made the principal distinction between these two species.³ As has been recently pointed out,⁴ this does not always hold true, and if it did, it would be at best a weak specific character. Many specimens of *J. horizontalis* show two generations of fruit, but the writer has been unable to determine whether or not this is always the case.

Character 8. The fruits of *J. virginiana* average smaller (2.0–6.5, mostly 3.5–5.5 mm. long) than those of the other two species (4.5–8.0, mostly 5.5–6.5 mm. in *J. horizontalis* and 4.0–9.0, mostly 5.5–6.0 mm. in *J. scopulorum*), but individual fruits of *J. virginiana* may be larger than some individuals of the other two species. That this is a statistical difference, requiring the measurement of many fruits to identify a specimen, is shown in tables 1–6.

Character 9. The number of seeds in a cone was shown by Blake⁵ to be different in *J. virginiana* and *J. horizontalis*. Again, the character is statistical; the usually limited supply of cones on a specimen, and the time consumed by their dissection, make this character less practical than most of the others here listed. The present writer's observation is that *J. virginiana* has 1–3 seeds per cone, *J. horizontalis* (1–) 2–6 seeds per cone, and *J. scopulorum* 1–4 seeds per cone.

Character 10. The long, deep pits on most (but not all) of the seeds of *J. scopulorum* serve to distinguish this from the other two species. Nearly all the seeds of *J. virginiana* are pitted;⁶ about half the seeds of *J. horizontalis* are pitted. Seeds are best prepared for examination by picking the cones to pieces then dipping the seeds in alcohol and rolling between the fingers to remove adherent resin.

The facts outlined above have been derived from the study of mass collections from the following localities:

J. virginiana: MAINE; York Corner. NEW HAMPSHIRE; Hampstead, Derry. VERMONT; Colchester. MASSACHUSETTS; Newbury, Bedford, Hopkinton. CONNECTICUT; Portland. NEW JERSEY; Pompton Lakes, Darlington. VIRGINIA; Strasburg. WISCONSIN; Dykesville, Hartland, Janesville, Coon Valley. MICHIGAN; Quincy. TENNESSEE; Bradford. GEORGIA;

³ Sargent, Gard. & For. 10: 420. 1897.

⁴ Morton, Rhodora 43: 347. 1941.

⁵ Blake, Rhodora 12: 218. 1910.

⁶ See Am. Jour. Bot. 30: 474. 1943.

Cartersville. MISSISSIPPI; Corinth. MISSOURI; Gray Summit (collected by Dr. Edgar Anderson). FLORIDA; Santa Rosa Island. KANSAS; Sedan (collected by H. A. Stephens & L. H. Shinnors), Riley Co. (collected by Frank C. Gates). ARKANSAS; Busch.

J. horizontalis: MAINE; Monhegan Island, Tenents Harbor. ONTARIO; Great Cloche Island, Little Current. MICHIGAN; Point Seul Choix. WISCONSIN; Baileys Harbor. WYOMING; Ranchester.

J. scopulorum: SOUTH DAKOTA; Upper Tunnel in the Bad Lands, Wasta, Interior. MONTANA; Bridger. WYOMING; Mammoth Hot Springs in Yellowstone Park, Burris.

In addition, the sheets of *J. horizontalis* and of *J. scopulorum* in the Arnold Arboretum, of *J. horizontalis* from Newfoundland in the Gray Herbarium, and of *J. virginiana* in the herbaria of the University of Wisconsin, Kansas State College, the University of Minnesota, and North Dakota Agricultural College, were examined for the characters listed above.

Certain representative data concerning three of these characters have been selected and presented in tables 1-6. In table 1, the epidermal cells in this colony of *J. virginiana* are seen to vary on each individual from 5 μ to 15 or 20 μ in width, and the averages to vary from 9.5 to 12.0 μ per individual. Since each average represents but 30 cells its significance is limited. The average of the 300 cells measured for the colony is 11.0 μ . In table 2, there is even a greater spread in averages for each plant, but the average for the colony is 10.2 μ , reasonably close to that in table 1. The lowest average for a colony of *J. virginiana* was 10.0 μ , and the highest 11.4 μ . For table 3, the measurements of nearly 2000 cells were averaged, to give a figure of 10.9 μ . The mode for every colony, and for every individual, is 10 μ in *J. virginiana*. Turning to *J. horizontalis*, where the mode for the individual is usually 15 and rarely 20 μ , we find in table 4 a range of 15.5-20.2 μ for averages of individual plants, with an average of 17.5 μ for the 300 cells measured from the colony; in table 5, representing 10 herbarium sheets from a single province of Canada, the individual plants range from 13.8-17.5 μ average widths, and the grand average is 15.4 μ . So, the results are the same whether we take 10 individuals from one patch, or 10 individuals from different localities; this illustrates the principle stated in italics in the fourth paragraph of this paper. The six mass collections of *J. scopulorum* showed similar variability of individuals and uniformity of colonies, therefore but one is described (table 6).

Examining now the character of straight vs. hooked cone-bearing peduncles, we find again considerable variation between individuals and uniformity of colonies. In table 2, the count, for the third plant in the list, of 35 straight peduncles against no curved ones is fair indication of nearly or quite complete lack of curved peduncles, yet on other twigs from the same colony may be found as many as one fourth of the twigs hooked. But, as was the case when epidermal cells were studied, the averages for the two colonies described in tables 1 and 2 are very similar (10 and 9 per cent, respectively), and close to what is found when 600 peduncles are examined (table 3). And again, variable as are the percentages for individuals of

J. virginiana, they never approach those of the equally variable *J. horizontalis* (tables 4, 5). The averages for individual trees of *J. scopulorum* overlap the higher figures of *J. virginiana* and the lower ones of *J. horizontalis*, but *J. scopulorum* is amply distinct from the others on a different set of characters.

SUMMARY

A study based on mass collections made throughout much of the ranges of *Juniperus virginiana*, *J. horizontalis*, and *J. scopulorum*, as well as on herbarium material, shows that these three species are always clearly recognizable on a number of characters, except when two species grow together, that the variation within each species is often more conspicuous than, but never as constant as, the variation which separates species, and that many of the distinguishing features are, while perfectly practical for the taxonomist, statistical in nature.

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TAXONOMY AND DISTRIBUTION OF THE GENUS
CERCIS IN CHINA¹

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The genus *Cercis* is widely distributed in the North Temperate Zone and, because of its discontinuous distribution, occurring as it does in southeastern Europe and adjacent parts of Asia, in eastern Asia, and in North America from New England to Michigan and California southward to Mexico, it is of special interest to the phytogeographer. This is a rather remarkable case of discontinuous distribution. It has been accepted that there is a lesser development of the genus in eastern Asia than in the other Eurasian and North American centers, with but two or three species occurring within a restricted area in central China. However, recent botanical explorations in China have increased the number of species as well as the geographic range of the genus in China, which involves a certain revision of our previous concepts of the group. The genus is a small one, a total of about twenty-five species having been described, more than one-third of which have been reduced to synonymy. It is suspected that too many species have been described from North America, for of the seven species proposed by Greene in 1912, Small in 1933 recognized none from the southeastern United States (at least two being from the range of Small's *Flora of the Southeastern United States*), while Jepson in 1936, in his *Flora of California*, reduced both of Greene's Californian species to *Cercis occidentalis* Torr. There are probably not more than about a dozen valid species of the genus now known.

This taxonomic study of the Chinese species is based on the material preserved in the herbarium of the Arnold Arboretum of Harvard University. Five species are recognized: *Cercis racemosa* Oliver, *C. Chuniana* Metcalf, *C. chinensis* Bunge, *C. Chingii* Chun, and *C. pauciflora* Li; and these are enumerated below with citations of all specimens examined. Among these, four are of rather limited occurrence. Only one, *C. chinensis* Bunge, is widely distributed in China, and in this respect can be considered as the counterpart of *C. Siliquastrum* L. of southern Europe and *C. canadensis* L. of North America.

Cercis chinensis Bunge occurs throughout the temperate regions of China from southern Kansu and southern Shensi in the northwest, eastern Sikang and northwestern Yunnan in the southwest, to northern Kwangsi in the

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south, Fukien, Chekiang, and Kiangsu along the coast in the east, and finally to Shantung and Honan in the northeast. Within this great circle there are only two provinces, Kiangsi and Hunan, wherein the species is not definitely known to occur.

It is evident, from the number of collections made and the data in the form of field notes, that this species occurs most abundantly in the hilly districts of western Hupeh and eastern Szechuan. Wilson, ex Craib in

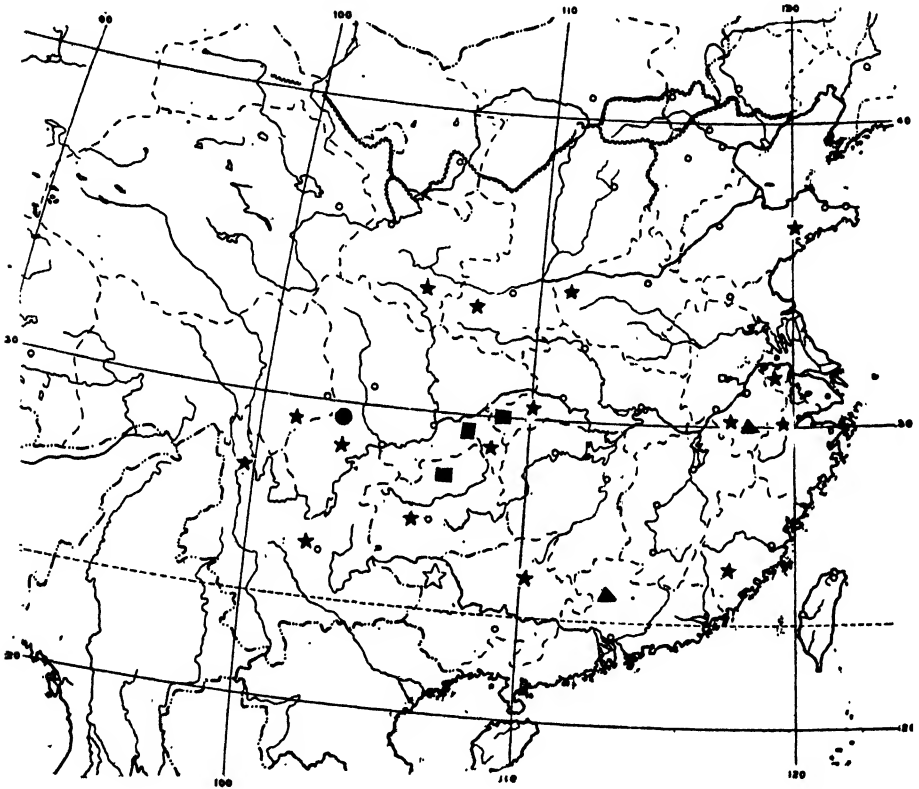


FIG. 1. Distribution of *Cercis* in China: Squares, *C. racemosa*; outlined star, *C. Chuniana*; solid stars, *C. chinensis*; triangles, *C. Chingii*; circles, *C. pauciflora*.

Sargent, Pl. Wils. 2: 87 (1914), notes that it is very common in the latter regions. This area may thus be considered as the center of development of the species. The northern extension of the species is along the Tsinling Range, and thus 35° N is the approximate northern limit of its range. However, it is cultivated farther north in Peiping, which is about 40° N, and it is from the plants cultivated in that city that Bunge first described the species. It is also cultivated in various other localities in China from Peiping southward to Canton, and also in Japan, but is not indigenous to the latter

country. The natural habitat of the species is limited in eastern China to the hills along the western borders of the coastal provinces Kiangsu and Chekiang. In the south it is found in Fukien, northern Kwangsi, Kweichow, and northern Yunnan, with 24° N as its approximate southern limits. It is not found, except in cultivation, in the tropical southern part of Kwangtung, Kwangsi, and Yunnan; it is not recorded from Hainan, nor from Indo-China. In the west it occurs along the eastern border of the great Tibetan Plateau, in the mountains of northwestern Yunnan and eastern Sikang. Apparently the Himalayas and the Tibetan Plateau stand in between the species of eastern and central Asia, for continuous distribution of the genus in Asia does not exist.

In eastern Asia, this species is essentially a temperate-zone tree occurring in hilly districts. It is found in open country, and in thickets and woodlands, generally along the slopes up to an altitude of 1200 m., although in the high plateau in farther western China, it may occur at slightly higher elevations.

The other four species are all restricted in distribution. *Cercis racemosa* Oliver is common in western Hupeh especially in Fang Hsien, where, according to Wilson, it occurs in moist woods between an altitude of 1200–1800 m., at a higher level than *C. chinensis* Bunge. The only other collections of this species noted are from eastern Szechuan, adjacent to western Hupeh, and in northwestern Kweichow, also close to Szechuan. *C. Chuniana* Metcalf is localized in the northern part of Kwangsi Province. This is a tree of about 10 m. high, found in open woods at an altitude of about 1200 m. *C. Chingii* Chun has been recorded from two different localities, one in southern Anhwei, and another in northern Kwangtung. *C. pauciflora* Li is known only from Mount Omei in Szechuan Province, where it occurs at an altitude between 800 to 1600 m. (fig. 1).

KEY TO THE CHINESE SPECIES OF CERCIS

- A. Inflorescences racemose, peduncles 2.5–10 cm. long.
 - B. Leaves ovate-reniform to suborbicular, symmetrical; peduncles slightly puberulous 1. *C. racemosa*.
 - BB. Leaves rhomboidal-ovate, inequilateral; peduncles glabrous 2. *C. Chuniana*.
- AA. Inflorescences clustered, not pedunculate.
 - B. Leaves ovate-reniform to suborbicular, large, about 7–15 cm. across; flowers preceding the leaves.
 - C. Pods thin, to 15 cm. long and 1.5 cm. broad, winged along one margin, straight and usually not dehiscent 3. *C. chinensis*.
 - CC. Pods coriaceous, to 6.5 cm. long and 1.2 cm. broad, dehiscent, the valves twisted, not winged 4. *C. Chingii*.
 - BB. Leaves subtriangular-ovate, small, to 6 cm. long and 5 cm. broad; flowers appearing with the leaves 5. *C. pauciflora*.

1. *CERCIS RACEMOSA* Oliver in Hook. Ic. **19**: pl. 1894. 1889; Diels, Bot. Jahrb. **29**: 409. 1900; Schneider, Ill. Handb. Laubh. **2**: 4: f. 2 a, b, 3 a. 1907; Craib in Sargent, Pl. Wils. **2**: 88. 1921; Chun, Chinese Econ. Trees 180.

1921; Rehd. Man. Cult. Trees Shrubs 482. 1927; ed. 2. 485. 1940; Stapf, Bot. Mag. 156: pl. 9316. 1933.

HUPEH: Western Hupeh, *E. H. Wilson* 607 (Veitch Expedition), May, 1900; Fang Hsien, *E. H. Wilson* 314, May, 1907 (flowers), Aug., 1907 (fruits), Sept., 1907 (fruits), a tree 15-30 ft. high, with much-branched head, in woods, alt. 4-5500 ft., flowers rosy pink; same locality, *E. H. Wilson* 707, Oct., 1907, a tree 10-35 ft. high, in woods, alt. 4-5500 ft. SZECHUAN: Wushan, *A. Henry* 5602 (ISOTYPE). KWEICHOW: Pichieh, *Y. Tsiang* 3939, Sept., 1930, a large shrub 20 ft. high, along road side, in fruit.

This species is strongly characterized by the loosely racemose inflorescences (about 2.5-10 cm. long), and the leaves hairy on the under surfaces.

Wilson notes (ex Craib, l.c.) that "This remarkable tree is fairly common in the moist woods of central Fang Hsien between 1200-1800 m. alt., but is extremely rare elsewhere in western Hupeh and has not been reported from any other province. It is a low-growing tree, seldom, if ever, more than 12 m. tall, with a simple trunk from 1 to 2 m. in girth near the ground, and a widespreading head from 4 to 10 m. though of relatively thin branches. . . . It is essentially a cool temperate tree and in western Hupeh always at higher altitudes than *C. chinensis* Bunge."

The type locality, as noted above, is in the eastern part of Szechuan closely adjacent to western Hupeh. The Kweichow plant cited above is a fruiting specimen with the pods detached, but the hairy leaves clearly indicate that *C. racemosa* Oliver is represented. The species occurs in cultivation in some parts of the United States and in Europe.

2. *CERCIS CHUNIANA* Metcalf, Lingnan Sci. Jour. 19: 551. f. 2. 1940.

KWANGSI: Northern Luchen, near the border of Kweichow, *R. C. Ching* 6188 (TYPE), June, 1928, a tree 30 ft. high, in open woods, alt. 3800 ft., pods purplish, drooping; Shuen-yuen, *Z. S. Chung* 81566, May, 1936, a tree 10 m. high, in woods, pods young, red; Chuen Yuen, *Z. S. Chung* 81984, June, 1937, along stream side, pods 9-10 cm. long, seeds 3-8.

Metcalf did not have flowers when he described the species, stating: "Inflorescences of small racemose branchlets with usually two-five fruits." In *Chung* 81566, there are inflorescences bearing very young fruits. These racemes measure 3.5-5 cm. long and bear many (10-15) flowers. The racemes usually become much shorter in the fruit, as is also true of those of *Cercis racemosa* Oliver.

In the racemose inflorescences, this species is allied to *Cercis racemosa* Oliver. But the peduncles, which Metcalf did not note, are glabrous in *C. Chuniana* Metcalf but puberulous in *C. racemosa* Oliver. Moreover, *C. Chuniana* Metcalf differs from Oliver's species in the pods being only very narrowly winged along one margin and the leaves being rhomboidal-ovate and very unequilateral. In the pronouncedly unequilateral leaves, a character that was not noted by Metcalf, this species is distinct and unique in the genus.

3. *CERCIS CHINENSIS* Bunge, Mém. Sav. Êtr. Acad. St. Pétersb. 2: 95. 1833; Hemsley, Jour. Linn. Soc. 23: 213. 1887; Pampanini, Nuov. Giorn. Bot. Ital. II. 17: 393. 1910; Craib in Sargent, Pl. Wils. 2: 87. 1914; Chun, Chinese Econ. Trees 178. pl. 66. 1921; Small, Addisonia 6: 33. pl. 209. 1921; Chung, Mem. Sci. Soc. China 1: 106. 1924; Rehd. Jour. Arnold Arb. 7: 152. 1926; Rehd. & Wils. op. cit. 8: 127. 1927; Chun, Sunyatsenia 1: 253. 1934.

Cercis japonica Sieb. ex Planch. Fl. Serres 8: 269. pl. 849. 1853.

Cercis glabra Pampanini, Nuov. Giorn. Bot. Ital. II. 17: 393. f. 9. 1910; Bull. Soc. Tosc.ortic. 36: 215. f. 16. syn. nov. 1911.

HOPEI: T. N. Liou 1228, 1229. SHANGTUNG: C. Y. Chiao 2430, 2818. KIANGSU: R. C. Ching 4884, Ching & Tso 417, Y. L. Keng 2597, C. L. Tso 945. CHEKIANG: Tang & Hsia 459, Y. L. Keng 847. ANHWEI: A. N. Steward 2306, R. C. Ching 3145, HONAN: J. Hers 291, 404, 525, 579. SHENSI: J. Giraldu s.n., J. Hers 2443, 3042, G. Fenzl 254. KANSU: F. N. Meyer 1642, 1935. HUPEH: A. Henry 7662, C. Sylvestri 1049, 1052 (SYNTYPE of *C. glabra* Pampanini, photo.), 3043, E. H. Wilson 501, 761, H. C. Chow 146, 593, W. Y. Chun 4143. SZECHUAN: A. Henry 7662 B, Bock & Rosthorn 1640, J. F. Rock 12041, W. P. Fang 10203, 22390. SIKANG: C. Y. Chiao 231. YUNNAN: G. Forrest 23223, 26273, 27194, J. F. Rock 8918, 9409, R. C. Ching 20583, K. M. Feng 2666, T. T. Yü 21075, W. C. Cheng 11000. KWEICHOW: H. Handel-Mazzetti 163, S. W. Teng 90029 A, 90029 B. KWANGSI: H. Fung 21190. FUKIEN: H. H. Chung 1243, 4833, 6972.

Dunn and Tutchet, Kew Bull. Add. Ser. 10: 90. 1912, credit this species to Kwangtung Province, Lienchow River, but this apparently represents a misidentification of *Cercis Chingii* Chun.

This species was first described by Bunge from cultivated plants in Peiping. It appears to be indigenous and widely distributed in temperate China. It is most abundant in western Hupeh and eastern Szechuan, which region may be considered as the center of distribution of the genus in general and of this species in particular. Wilson (ex Craib, l.c.) notes that "In western Hupeh and eastern Szechuan this beautiful flowering tree is very common but we never met with it wild west of the Red Basin of Szechuan. It occurs in open country, and in thickets and the margins of woods up to 1200 m. altitude. . . . This tree grows from 6 to 15 m. tall and has a moderately thick trunk clean of branches for half its height and a flattened rounded head." However, it has since been collected, as noted by the cited specimens above, in western Szechuan.

Wilson also notes "The flowers vary from pale pink to red pink and are produced in great numbers on all parts of the tree including the old branches and main trunk." In one of the collections cited above, J. F. Rock 12041 from Ching-chuan, western Szechuan, it is indicated on the field notes: "flowers white." This is the only collection noted for white flowers.

It is observed that among the assorted specimens of the species from different localities, while in general being very uniform in their characters, slight variations are found in the length of the pods and the pubescence of the leaves and pods. In most instances the leaves are completely glabrous, while in others they are slightly pubescent along the veins near the base on

the lower surface. Pampanini (l.c.) referred some of Sylvestri's specimens from western Hupeh with their leaves slightly pubescent below to *C. chinensis* Bunge, and three other specimens with completely glabrous leaves as representing a new species, *C. glabra* Pamp. Wilson (l.c.) notes that he is doubtful if *C. glabra* Pampanini is anything more than a mere form of *C. chinensis* Bunge. Type material of Pampanini's species, including a photograph of Sylvestri 1052, fragments of leaves and fruits of 1052 a, and fragments of flowers of 1051, all from the Biondi Herbarium, Florence, are now available for study. It is found that such a variation in pubescence is common in other specimens and that age is also a factor. I do not consider that Pampanini's species is a valid one, and it is accordingly reduced to synonymy.

A more definite variation, in the pubescence of the pods, is, however, present. Among the fruiting specimens from the provinces of Chekiang, Anhwei, and Kiangsu, and the cultivated plants from Tsingtao, Shantung Province, and Peiping, Hopei Province, it is found that they are very finely pubescent throughout. But the ovaries of the few flowering specimens from these same regions appear to be glabrous as in the other specimens cited. The pods are also of relatively shorter length in general, but some have long pods; and short pods are not uncommon in plants from other regions. In other characters these plants agree exactly with plants from other regions except one specimen, *T. Tang & W. Y. Hsia 459*, that has leaves puberulous throughout on both surfaces and rather conspicuously so on the lower surface. It appears that a form geographically located in eastern China and cultivated elsewhere is represented. As Bunge described the species from plants cultivated in Peiping, it may be that this pubescent form is the typical form of the species while plants from other parts of China represent another form. However, it is felt that any attempt to divide this species into forms or varieties should be based on actual observations of living specimens in the field.

This species, like *Cercis racemosa* Oliver, is cultivated in Europe and in various parts of the United States, being hardy as far north as the southern part of Massachusetts.

4. *CERCIS CHINGII* Chun, Jour. Arnold Arb. **8**: 20. 1927; Rehd. & Wilson, Jour. Arnold Arb. **8**: 127. 1927; Chun in Hu & Chun, Ic. Pl. Sin. **2**: pl. 82. 1929, Sunyatsenia **1**: 253. 1934.

Cercis chinensis sensu Dunn & Tutchet, Kew Bull. Add. Ser. **10**: 90. 1912; non Bunge.

ANHWEI: East of Hweichow city, *R. C. Ching 3332* (TYPE), Sept., 1925, a fairly common gregarious shrub along roadsides in the open. Also recorded from northern Kwangtung (Chun, l.c., 1934).

In its general habit, this species closely simulates *Cercis chinensis* Bunge. It is characterized by the thickly coriaceous pod, which is not winged at the

margin, but is dehiscent, and its valves somewhat twisted, when mature. The seeds are few (3-6), about 7-8 mm. long and 4-5 mm. wide, and imbedded in a thick whitish spongy tissue.

Chun says that "According to the late Dr. Stapf, some other genus might be represented. The dehiscent pod of the species is anomalous in *Cercis*." However, it is noted that in some very mature fruits in *Cercis chinensis* Bunge, the pods also dehiscence along one or both margins (examples: *Wilson 761* and *K. M. Feng 2666* cited under *Cercis chinensis* Bunge above).

5. *Cercis pauciflora* Li, sp. nov. Frutex, ramulis cinereis, ramulis novellis brunneis, elenticellatis; foliis chartaceis, longe petiolatis, subtriangulariter ovatis, 4-6 cm. longis, 5 cm. latis, acutis vel acuminatis, basi truncatis vel leviter subcordatis, supra viridibus, subtus pallidioribus, utrinque glabris, nervis primariis 5-7, gracilibus, supra subconspicuis, subtus elevatis, rete venularum utrinque subconspicuo; petiolo gracile, 2-2.7 cm. longo, apice leviter dilatato; floribus axillaribus cum foliis coetaneis, in ramis biennibus vel vetustioribus dispositis, 1-3-fasciculatis, bracteis ovatis minutis, 1.5 mm. longis, margine pubescentibus, pedicellis brevibus, saltem 3 mm. longis, glabris; calycis tubo cupuliformi, 4 mm. alto, 3 mm. lato, plus minusve irregulariter 5-lobato, lobis rotundatis, 1 mm. diametro, margine ciliatis; corolla rubra, vexilli ungui lineari 3 mm. longo, lamina reflexa oblongo-elliptica 4-5 mm. longa, maculis atrorubris adspersa, alis forma magnitudine similibus, patentibus, emaculatis, carina cymbiformi, apice rotundata, 1.1 cm. longa, ungui gracili brevi; staminibus 10, filamentis liberis, 8-9 mm. longis, antheris atrorubris; ovario plus minusve lineari, 3-4 mm. longo, glabro, stylo 6-7 mm. longo, stigmatibus inconspicuis.

SZECHUAN: Mount Omei, *F. S. Liu 1700* (TYPE), Oct., 1937, a shrub, alt. 800-1600 m., in flower.

In its vegetative characters, this species is characterized by the relatively small, subtriangular-ovate leaves. It differs from *Cercis chinensis* Bunge, in addition to its vegetative characters, in the fewer (1-3) flowers in each cluster with much shorter pedicels (scarcely 3 mm. long). In *Cercis chinensis* Bunge the flowers are usually 4-10 or more together and the pedicels 1.5-3 cm. long. Moreover, the calyx-tube of *C. chinensis* Bunge is broadly open above with more or less triangular lobes which are generally not ciliate along the margins; while in this new species the calyx-tube is not broadened above, and its rounded lobes are distinctly ciliate along the margins. This new species is furthermore characterized by the fact that the flowers appear in the fall when the leaves are fully mature. This autumn flowering may be or may not be a regular condition, but nevertheless, the other characters of the plant indicate that an undescribed species is represented.

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A PRELIMINARY CONSIDERATION OF THE BIOSYSTEMATY OF OXYCOCCUS

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The cranberries are a compact group of the *Vaccinieae*, with a circum-boreal distribution. Any decision whether they should be treated as the separate genus *Oxycoccus*, or as a section, or subgenus of *Vaccinium*, must await a more thorough investigation of the phylogeny of the entire group than is now available. Certainly, if this group is to be recognized as a genus, then a number of genera should be segregated from within what is now the widespread and polymorphic genus *Vaccinium*. The fact that the name *Oxycoccus* has been used in the present title and discussion does not necessarily indicate that I have come to a personal decision on the matter; it was done primarily because the group is so treated in the majority of current European and American works.

For well over a decade I have been attempting to arrive at some satisfactory solution of the problems which the systematics of even this small group presents. During this time, several papers of considerable interest have appeared. One of these, by Porsild (1938), was a taxonomic treatment of the Canadian material, although it actually dealt with all recognized species. The other, by Hagerup (1940), contained a cytological analysis of the European populations, and something of their ecology. Recent work on certain American materials (Darrow, Camp, Fischer & Dermen, in preparation) brought to light additional information which warranted a further discussion of the group.

In his systematic treatment, Porsild recognized four species and one variety. An additional entity—"gigas"—was noted by Hagerup.¹ By combining these two treatments with the findings of the chromosome complements of American material as reported by Darrow, Camp, Fischer & Dermen, the following cyto-taxonomic picture of the group may be obtained:

<i>Oxycoccus macrocarpus</i> (Ait.) Pers.	2n = 24.
<i>Oxycoccus microcarpus</i> Turcz.	2n = 24.
<i>Oxycoccus quadripetalus</i> Gilib.—"typical" material	2n = 48.
<i>Oxycoccus quadripetalus</i> var. <i>microphyllus</i> (Lange) M. P. Porsild ..	2n = 48.
<i>Oxycoccus ovalifolius</i> A. E. Porsild ²	2n = 48.
<i>Oxycoccus</i> "gigas"	2n = 72.

¹ Although Hagerup treated this entity as a binomial in the text, it was not set up in a manner entirely satisfactory to the present Rules of Nomenclature; where used in this discussion, the name will appear in quotation and without italics.

² Based on *Vaccinium oxycoccus* var. *ovalifolium* Michx., considered by Porsild—following a former decision of Robinson & Fernald (*Rhodora* 11: 54. 1909.)—to be an earlier

Having previously made field observations of the material in eastern North America, the mid-continent area, and in British Columbia, and thus—with the exception of *O. microcarpus*—having seen considerable amounts of the entities listed for North America growing under natural conditions, I was in general accord with Porsild's treatment when it appeared. However, the recent findings of the cytological condition within the cranberries—together with an increased understanding of the factors of speciation in the *Vaccinieae* in general—have led me to a preliminary consideration of the biosystematy of the group, the results of which are presented here. A definitive report must await the accumulation of considerably more data than are now available. In reviewing the situation, the following items should be noted, for they have played a prominent part in the interpretation of specific lines:

1. A considerable amount of controlled breeding work indicates that there are almost no sterility barriers between homoploid individuals and species in *Vaccinium* subgenus *Cyanococcus* (Darrow & Camp, in preparation). While it does not necessarily follow that the same situation is equally true in *Oxycoccus*, there are reasons to believe that such is the case.

2. A species which has arisen either through allopolyploidy or by hybridization is likely to be highly segregative. With time, various of the segregate forms may be differentially selected by environmental forces; that is, the segregate forms may be unequally successful in various habitats. A recent paper by Camp & Gilly (1943, p. 342-348) may be consulted for a more detailed discussion of the origin and development of allopolyploid and mictonic species.

In reviewing the North American material, it is obvious that the diploids (*O. macrocarpus* and *O. microcarpus*) are easily separable, each reasonably homogeneous and, today, distributionally disjunct. On the other hand, when sufficient material is examined, the tetraploids are found to be variable, and to intergrade to the extent that the entities defined would seem to have doubtful significance; certainly, they are difficult to separate with any degree of precision. As a group, the American tetraploids not only occupy the region between the present diploids, but also overlap the ranges of both to a considerable extent. It is also considered to be significant that the bulk of the tetraploid population combines the characters of both diploids, whereas the extremes tend toward one diploid or the other, thus fulfilling the expected variability of a segregative population.

Since it seems likely that the individuals of the tetraploid population are interfertile and, as will be pointed out later, there is evidence that no more

name for *Vaccinium oxycoccus* var. *intermedium* Gray, a plant supposed to be of the American Pacific Northwest and northeastern Asia. It is doubtful whether a careful reanalysis of the types would indicate that they were precisely equal. Porsild's paper may be consulted for the general synonymy of the group.

than a generalized geographic segregation has taken place among them, it is thought best to consider them as members of a single species. The two diploid populations will be treated as distinct species. In order to expedite our later discussion, brief descriptions of the more easily visible diagnostic characters of these species are presented here together with a summary of their distributions, these given in detail only for North America.

OXYCOCCUS MACROCARPUS (Ait.) Pers. A diploid species ($2n = 24$).

Leaves flat or only slightly revolute, elliptic-oblong, apically rounded, 5–15 mm. long, 2–8 mm. wide. Flowers 2–6, solitary in the axils of the lower bracts or basal leaves of a normal leafy branch. Pedicels pubescent, bearing a pair of green bracts above the middle, or even subtending the fruit; bracts usually leaf-like, 2–4 mm. long (forms are known with minute, red, scale-like bracts 1.5 mm. long). Calyx lobes triangular-acute, sometimes obtuse. Fruit 10–20 mm. thick, generally deep pink to red, tartly acid.

Distribution: North America; estab. in Europe, probably first as a ballast waif, sometime prior to 1869. In North America: Minnesota, eastward to Newfoundland, south to Tennessee and North Carolina; reported by Small (Man. 1933) from Arkansas. Extensively cultivated in eastern North America and to some extent along the Pacific coast, where it is said to have escaped.

OXYCOCCUS MICROCARPUS Turcz. A diploid species ($2n = 24$).

Leaves strongly revolute, ovate when flattened, apically pointed, 2–6 mm. long, 1.5–2 mm. wide. Flowers 1–2(3), in a determinate inflorescence, the result of abortion of the vegetative portion of the branch. Pedicels glabrous, bearing a pair of red bracts below the middle; bracts scale-like, 0.5–1 mm. long. Calyx lobes relatively short, rounded to obtuse, or sometimes mucronate. Fruit 5–7 mm. thick, pink, insipid.

Distribution: Iceland, Europe, Asia, and northwestern North America; unknown from Labrador and Greenland. In North America: Alaska to British Columbia and Alberta (Queen Charlotte Isl., and in the mts. to about 51° Lat.), eastward to northern Saskatchewan and parts of the Northwest Territories. Reported by Porsild from the east shore of Hudson Bay.³

O. QUADRIPETALUS Gilib. A tetraploid species ($2n = 48$).

Leaves flat to strongly revolute, narrowly to broadly elliptic-ovate, apically acute to obtuse, or rarely somewhat rounded, 2–10 mm. long, 1.5–5 mm. wide. Flowers (1)2–3(4) in a determinate inflorescence, or at the base of a weak branch which soon dies, or at the base of a strong vegetative branch which continues growth. Pedicels pubescent (sometimes obscurely so), bearing a pair of red bracts below, at, or above the middle; bracts scale-like, 0.7–1.5 mm. long. Calyx lobes variable, generally obtuse or mucronate, sometimes rounded, or occasionally triangular-acute. Fruit 7–13 mm. thick, pink, or pink flecked with red dots or stripes, or sometimes red, sub-acid to acid.

Distribution: Europe, Asia, North America, and Greenland; unknown from Iceland. In North America: Alaska, eastward to Great Slave Lake and

³ Although a logical extension of range, this material may yet prove to be a "microcarpoid" segregate of *O. quadripetalus*, the common form in Labrador and Greenland.

Labrador, south to n. California, n. Idaho, Minnesota, ne. Ohio, and New Jersey.

Since Porsild recognized two species (one with a variety) in what I now consider to be a single tetraploid species, it would be well to discuss this material in some detail. In the first place, one must assume from his discussion and key that the lack of a well developed pubescence on the pedicel and a relatively large leaf were the more important factors in the recognition of *O. ovalifolius*. In examining a fairly large series of plants I find some which answer the description of this species as delimited, but even in the Pacific Northwest much of the material has a conspicuous pedicellary pubescence and would seem better placed in the large-leaved phase of *O. quadripetalus*. Therefore, it would seem more expedient not to maintain *O. ovalifolius* as a species.

Let us consider, then, the entire tetraploid population and determine whether it can be broken down into subsidiary segments. If it can—and if the population is segregative—there should be a series of recognizable morphological groups. But first as to the method of analysis. Since the tetraploid population apparently has been derived in some manner from a combination of the diploids, we may legitimately use the contrasting characters of the diploids in making our separations. Among the more conspicuous of these, the following might be listed: “basal” vs. “determinate” inflorescence, “large” vs. “small” leaf,⁴ pubescent vs. glabrous pedicels. It is naturally a matter of opinion whether these are the most important characters, but they are as obvious as any and will suffice to begin the study.

Although individual specimens may occasionally give trouble, the bulk of the tetraploid material can be easily separated into two groups, one with a “macrocarpoid” inflorescence, the other with a “microcarpoid” inflorescence.⁵ Likewise, although somewhat more arbitrary, there are such marked differences in leaf size and shape that each of the groups already set up can be divided into “large-leaved” and “small-leaved” subgroups (again, “macrocarpoid” vs. “microcarpoid”). Since, by definition, the pedicels of this material are never completely glabrous, a further “macrocarpoid” vs. “microcarpoid” separation can be made only on the basis of dense pubescence vs. scattered or obscure pubescence. Again, by using arbitrary limits, additional separations may be made. Thus, if a sufficiently large amount of material is available, eight reasonably distinct classes of segregate forms may

⁴ The terms “large” and “small” as used here in reference to the leaf do not mean size only; in this instance, differences in length-width ratios, and relative amount of surface involved in the revolute margin, as well as the actual over-all surface area, are the determining factors in the separation of the “large” (“macrocarpoid”) and “small” (“microcarpoid”) leaf types.

⁵ A number of years ago, Fernald (1902) called attention to this type of variation.

be recognized, each yielding to identification by a key no more complicated or difficult than that used in the differentiation of many species.

Nor are the foregoing the only characters which might have been used. Among the items which are equally diagnostic of the basic diploids under detailed examination, and which certainly should be used in any future critical and definitive analysis, are the following: (1) length-width ratio of the corolla lobe; (2) type and distribution of pubescence on the anther filament; (3) the relative exertion of the style at anthesis; (4) the shape of the calyx lobe; (5) the presence or absence of—and the relative conspicuousness of—the tuft of hairs at the apex of the calyx lobe; (6) the percentage of total surface involved in the revolute leaf margins; (7) the shape of the leaf apex; and even (8) the basic color and type of mottling on the fruit. With a brief search in any considerable amount of tetraploid material, individuals can be found which exhibit almost any combination of these characters. It is therefore obvious, when viewed in its entirety, that the tetraploid population has considerable morphological variability, indicative of a high degree of genetic segregation.

Our next problem is to determine whether sufficient selection pressure has been exerted on this segregative population to yield segments worthy of nomenclatural recognition. Frankly, I see no need to force the issue to its ultimate limits; the character of a segregative complex is such that we would soon find ourselves involved with the plants of a single locality, or even with individuals. Let us, therefore, for the present, pass over the lesser segregative groups and concentrate on the more generalized types, permitting a certain degree of complexity in each. We can, for example, consider the broadly defined “macrocarpoid” group of segregates—those with basal inflorescences, generally large and only slightly revolute leaves, and relatively pubescent pedicels—and, as a unit, consider its distribution. At first glance, it appears to be scattered, yet a closer examination reveals that it becomes a more prominent component of the tetraploid population as one goes southward.⁶ Nor is it limited to the Pacific Northwest and northeastern Asia, with a few casual outliers in mid-continent North America, as was originally supposed. In some restricted areas in eastern North America it appears to be the dominant form; and in New Jersey, at the southern limit of its range, it makes up about half of the general population. Conversely, although the “microcarpoid” segregates are notably concentrated along the northern margin of the tetraploid population, excellent examples are known from as far south as Long Island, N. Y. Much the same situation prevails in the mid-continent area and in the Pacific region where occasional “microcarpoid” plants may be found near the southern border of the complex.

⁶ An excellent example of the “macrocarpoid” phase of *O. quadripetalus* from California—labeled “*O. macrocarpos*”—may be found illustrated in a recent paper by Dayton (1938).

It is therefore apparent that the selective forces which brought about the geographical disjunction of the diploid populations of *O. macrocarpus* and *O. microcarpus* have also been operative within the tetraploid population. That the "macrocarpoid" and "microcarpoid" phases of the tetraploid have not achieved a greater degree of regional concentration and geographical isolation is probably to be explained by the fact that neither is genetically pure, each having a little of the other in its hereditary make-up. This may also explain why the tetraploid, *O. quadripetalus*, while occupying a much larger territory than either of its diploid ancestors, seems never to have been able to venture quite as far north as *O. microcarpus*, nor quite as far south as *O. macrocarpus*.

Let us now turn to the subspecific nomenclatural situation in *O. quadripetalus*. Because of its small leaves, there is a strong inclination to associate the "microcarpoid" phase with var. *microphyllus*. By arbitrary methods, the large-leaved phase (if limited to a "microcarpoid" type of inflorescence) might be taken to be the "typical" material. Using similar methods, we might conclude that var. *ovalifolium*⁷ was the equivalent of the "macrocarpoid" phase. However, to follow such a nomenclatural scheme with any degree of precision would necessitate the re-examination of type specimens, a thing which is impossible under present conditions. Furthermore, even if a complete set of type specimens were available the problem would not be solved, for the complex nature of the tetraploid population—if we were to approach it in any critical manner—would preclude any but a most complicated nomenclature. Because of this fact, I would suggest, at least for the present, if the binomial *Oxycoccus quadripetalus* is not sufficient for some particular purpose, that there be appended to it some term as the "macrocarpoid phase," the "microcarpoid phase," or the "median phase," depending upon the more obvious of the morphological characters exhibited by the material. Thus any possible nomenclatural errors resulting from a hasty application of names would be circumvented, until such time as the type specimens are again available. In fact, even then, I cannot see where much is to be gained by attempting to make too fine subspecific nomenclatural distinctions in this particular population. To increase the subspecific names to what appears to be a critical minimum would require considerably more material than is now available in herbaria, or is likely to accumulate in the near future and, even then, to do so might needlessly encumber the nomenclature of the species. On the other hand, to use the three most obvious subspecific groups, mentioned here as possibilities in *O. quadripetalus*, would simplify nomenclatural matters once the types were ascertained. But it must be admitted that such a procedure would result only in a broad systematic generalization lacking in critical details.

⁷ The combination, as a variety, seems never to have been made in *Oxycoccus*; hence the "um" rather than the "us" ending.

Thus far, we have been dealing only with the North American material of *O. quadripetalus*. Although the specimens available to me from outside this region are not overly abundant they are sufficient to make certain observations. On examining all the available material of this species one thing was obvious: it could be separated with relative ease into the "macrocarpoid phase," the "median phase," and the "microcarpoid phase," not only in North America, but also in northeastern Asia, north-central Asia, and Europe.⁸ It is therefore apparent that the population of *O. quadripetalus* is constant in one characteristic: it is highly segregative throughout its range.⁹

Having made some attempt to clarify the general picture of the two diploid species and the derived tetraploid, we may now turn to a discussion of the apparently sterile hexaploid, "gigas." The sterility of "gigas" appears to be caused by aberrancies during meiosis resulting in abortive pollen. So far, according to Hagerup, this material is known only from scattered stations in Denmark, Finland, and East Prussia. In looking back over my own field work in North America, I can recall occasional plants similar to *O. quadripetalus*, but somewhat coarser than usual, which seemed to be unfruitful. In going over the herbarium material, additional specimens have been found whose vegetative parts closely match those of the hexaploid plant illustrated by Hagerup. In various instances, these were either in flower ("gigas" flowers freely) or, if collected late in the season, bore no fruit. It is therefore probable that hexaploid plants are not unique in Europe, but also occur sporadically throughout the range of *O. quadripetalus* in Asia and North America.

Hagerup was somewhat of the opinion that these hexaploid plants were the result of hybridization between individuals of the tetraploid *O. quadripetalus* and the diploid *O. microcarpus*. Based on studies of the origin of hexaploids in *Vaccinium* (Camp 1942a; and Camp, in press), it would seem unnecessary to suppose that this is the case. In fact, it is unlikely. For the most part, the hexaploids of *Vaccinium* apparently have been derived out of tetraploid populations, sometimes highly heterozygous in nature. The mechanics seems to be the fusion of a normally reduced gamete with a non-

⁸ Something of the morphological complexity of the European population may be gleaned by consulting a series of papers by Gleisberg (1919, 1922a, 1922b). A continuation of such analyses today would necessitate co-ordinate cytological studies, for Gleisberg considered *microcarpus* to be only a varietal manifestation of the tetraploid population, nor did he know of the presence of the hexaploid "gigas."

⁹ On casual observation, one population would appear to be an exception; this is the material from Greenland, which seems to be mostly "microcarpoid." This, however, is no more than might be expected. Even so, after careful examination, it appears that there is considerably more variability in fundamental characters such as length-width ratios of the leaves, shape of the leaf apex, shape of the calyx lobes, and relative pubescence of pedicels than might have been anticipated, leading one to suspect that a larger series of specimens might uncover further segregate forms.

reduced gamete, thereby directly yielding a hexaploid individual. Nor would it seem necessary to speculate, as did Hagerup, on the problem of the dispersal of such material. There is ample evidence in *Vaccinium* that it is a repetitive process, and I see no reason to suppose that it happened only once in *Oxycoccus*, although it is admittedly interesting to consider the possibility of the European hexaploids as being parts of a single, widely dispersed clone. I fully expect that additional cytological work in Asia and North America will reveal other hexaploids. In fact, we should not be surprised if some of them prove to be fertile.¹⁰

There is perhaps one last point which might be brought up. That is the possible phyletic development within the group here under discussion. Of the known living diploids, *O. macrocarpus* seems to have retained the greatest number of primitive characters; in addition, it still persists in the region of the Southern Appalachian Mountains of North America, that great reservoir of Tertiary archetypes.¹¹ It is easy to suppose that *O. microcarpus* was derived directly from *O. macrocarpus* through reductions and tissue readjustments, the result of a series of mutations. The end product was a population considerably different from the ancestral form and able to migrate into new areas and persist under conditions which excluded the archetype.¹² This is an example of primary speciation.¹³

In considering the origin of the tetraploid population, there is no need to build up any complicated hypothesis as to its possible ancestors, for it exhibits no morphological characters which are not present in the two existing diploids. Therefore, we might conclude that it has arisen by a compounding of the heredities of *O. macrocarpus* and *O. microcarpus*. We have only to discuss the mechanics of its origin. Two alternative methods seem most likely:

1. Subsequent to the disjunction of the two diploid species, they were brought together along their margins by some climatic factor which forced a partial readjustment in range. Where they met, hybridization took place.

¹⁰ Three American species of *Vaccinium* are known to be hexaploid and completely fertile (Darrow & Camp, in preparation; and Camp, in press); in fact, about half of the acreage of the present commercial plantings of blueberries in the United States is of hexaploid material.

¹¹ It is in this region where one also finds the relatively primitive *Vaccinium erythrocarpum* Michx. (= *Schollera erythrocarpa* Steud.; = *Oxycoccus erythrocarpus* Pers.; = *Oxycoccoides erythrocarpus* Nakai; = *Hugeria erythrocarpa* Small) an erect shrub with deciduous leaves, but with a type of flower quite similar to that of *C. macrocarpus*. In the first paragraph of this paper it was mentioned that much yet needed to be done to establish satisfactory generic lines within the Vaccinieae.

¹² The advantages of a low-growing plant under subarctic conditions, where the ground may be swept almost free of snow, and where there is considerable browsing by large animals, has been mentioned in another place (Camp 1942b, p. 223, footnote 21).

¹³ The differences between primary and secondary speciation were briefly discussed in a previous paper (Camp 1942a).

Then, out of this hybrid population there arose a series of fertile allotetraploids. After this, another shift in climate took place which again separated the diploids, leaving the allotetraploid population in possession of the area where it arose. This would be the nuclear population out of which the present *O. quadripetalus* has spread.

2. After the geographic disjunction of the diploids, autopolyploids arose in each, forming effective independent reproductive tetraploid populations. That derived from *O. microcarpus* would have been less effective in the far North than the diploid because of its larger size, and so might have persisted as an effective population by migrating southward. Thus the tetraploids of *O. microcarpus* could have come into contact with those of *O. macrocarpus* and hybridized with them, the result being the nuclear element of the present population of *O. quadripetalus*.

Prior to a more careful analysis of the situation, it is difficult to determine which of these methods was responsible for the origin of *O. quadripetalus*, for either would be likely to yield a population which was potentially segregative and superficially quite similar in appearance. A recent paper by Dermen and Bain (1941) indicates that polyploid material can be experimentally produced in *O. macrocarpus*. It might be supposed, if polyploids can be induced with a certain degree of ease, that they are likely to occur in reasonable abundance under natural conditions, not only in *O. macrocarpus*, but also in *O. microcarpus*. This has not yet been found to be the case for either.¹⁴ However, the apparent absence of autotetraploids might be explained by assuming that they are "absorbed" by the tetraploid *O. quadripetalus* population about as fast as produced, since this species covers so much of the ranges of the diploids. This hypothesis might also be used to explain the concentration of the "microcarpoid" forms along the northern border of *O. quadripetalus*, and the similar concentration of "macrocarpoid" forms along its southern border. But, since *O. macrocarpus* is limited to eastern North America, this does not at all serve to explain the presence of the strong "macrocarpoid" element in the material of *O. quadripetalus* in western North America, Asia, and Europe; nor will it account for the even stronger "microcarpoid" element of *O. quadripetalus* in Labrador and Greenland, where *O. microcarpus* appears to be absent.

Conversely, when the two diploids are examined critically, examples may be found which indicate that these two populations, at some time, have exchanged genes. While by no means overly common, examples of *O. macro-*

¹⁴ Hagerup found no tetraploids in the European material of *O. microcarpus*. In the case of *O. macrocarpus*, we feel rather certain of our conclusion. Since this species is the standard commercial cranberry, it has been selected from the wild and extensively cultivated and bred in North America for many years. Naturally, the plants brought into cultivation were selected for their vigor, fruitfulness, and size of fruit, characteristics which, in the *Vaccinieae*, we have learned to associate with polyploidy. No single commercial variety of *O. macrocarpus* has yet been found to be other than diploid.

carpus are known with "microcarpoid" pedicellary bracts, others have atypical length-width ratios in the leaves, leaf apices which are "microcarpoid," or obtuse or mucronate calyx lobes. By the same token, *O. microcarpus* is not completely homogeneous; some individuals have atypical length-width ratios in the leaves, some have blunter leaf apices than normal, and some have mucronate calyx lobes; and one plant was found with an almost "macrocarpoid" type of inflorescence. Of course, it might be supposed that this is a residual condition in both; that is, a situation wherein the genetic segregation was not yet complete when the original geographic disjunction took place. However, on the basis of the material available, the aberrancies in *O. microcarpus* seem to be most pronounced in the North American population. In my opinion, this points to a period of hybridization along the margins of the ranges of the diploids subsequent to a period of geographic isolation and stabilization, rather than a condition of residual genes. It would have been during such a period when a population of allotetraploids could have arisen out of the hybrids. I therefore favor the hypothesis that *O. quadripetalus* is a segregative allotetraploid.

But no matter what may ultimately be found to be the method of origin of this tetraploid population, I should like to emphasize one point. It is not my opinion that *O. quadripetalus* is a species of recent origin, except in comparison to the age of the diploids. Its present wide distribution would indicate that it arose prior to the Pleistocene, at a time when the continental masses of Europe, Asia, and North America were more closely connected. Furthermore, it seems likely that this tetraploid arose on what is now the North American segment of Holarctica, migrating from there into Europe by way of northern Asia. It would therefore seem logical to suppose that the primary divergence of the diploids must have been in progress in what is now North America at an even earlier date, probably not later than the mid-Tertiary.

SUMMARY

Recent work indicates that the cranberries, a group of the *Vaccinieae* commonly recognized as the genus *Oxycoccus*, occur as diploids, tetraploids, and hexaploids. Today, the diploids exist as two geographically disjunct populations, on the whole easily separable by a series of well-marked morphological characters. The southern diploid species, *O. macrocarpus*, limited to North America, appears to be the basic form, and *O. microcarpus* the derivative which, since, has achieved a wide distribution in high, northern latitudes, being in North America, Asia, and Europe.

A third population, essentially circumboreal in distribution, is known to be present; it is tetraploid and combines the characters of the two diploids. Although considerably segregative—so much so that various species, varieties and forms have been previously described from within it—there is no

evidence that any of the segregate types, even as aggregate groups, have achieved sufficient geographical or ecological disjunction to be worthy of more than subspecific recognition. Therefore, it seems best to treat this tetraploid population as a single species—*O. quadripetalus*. Although there is evidence that certain of these groups have attained a degree of differentiation as a result of selection, it is doubtful whether more than a simplified subspecific nomenclature would be of value, and even this could not be applied in any really critical manner. A more detailed analysis—possibly resulting in a complex and cumbersome nomenclature—should not be undertaken until considerably more material and information is available concerning this population from its entire distribution.

Although hexaploid material is known from Europe, it seems not yet to have been given satisfactory nomenclatural treatment. So far, only isolated, sterile, hexaploid plants are known. Since they appear to have been derived directly out of the tetraploid and, on the basis of those studied, are distinguishable from it primarily by their larger size, there seems to be no logical reason—should the need arise—why these forms could not be nomenclaturally appended to *O. quadripetalus*. However, as was pointed out, there is ample evidence from *Vaccinium* that hexaploids in the Vaccinieae can be completely fertile. Should future work in those areas in Europe, Asia, and North America where hexaploids are known, or suspected, reveal the presence of fertile plants in the process of building up an autonomous population, there would then be reason for the recognition of such hexaploid material as a valid species.

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OCCURRENCE AND DISTRIBUTION OF THIAMINE, RIBO- FLAVIN, AND NIACIN IN AVENA SEEDLINGS¹

ILDA McVEIGH

Certain of the B vitamins have been found to increase during the early stages of germination of cereal grains (Burkholder and McVeigh 1942). The object of this study is to correlate the changes in vitamin content of *Avena* seedlings at various stages in germination with changes in dry weight; also to determine the content and distribution of these vitamins in the organs of the seedling at successive stages in germination. The study was restricted to thiamine, riboflavin, and niacin, since they are known to function as parts of enzyme systems, and are therefore likely to be causally associated with cell division and enlargement.

Because the young *Avena* plant is so often employed as the test organism for growth hormones, it has been the subject of many investigations. Its cellular development, particularly that of the coleoptile, is now well understood (Avery, Burkholder & Creighton 1937). A study of the presence and distribution of physiologically active substances within the developing plant has been made in an attempt to determine the effect of these substances on the development of the plant.

According to Avery, Burkholder and Creighton (1937) cell division in the embryonic *Avena* coleoptile starts within 24 hours after the seeds are placed under suitable conditions for germination, and continues with appreciable though diminishing intensity until the coleoptile is about 10 mm. long, or until about the third day of germination. As long as cell division persists, it goes on with equal intensity throughout the coleoptile. Further growth is due almost entirely to elongation of cells.

Thimann (1934) reports that the amount of auxin in the *Avena* coleoptile decreases steadily with distance from the tip. The concentration of auxin per unit length of the root tip is somewhat less than in the coleoptile tip, but is about the same in the root base as in the coleoptile base. The decrease with distance from the tip is comparable in the two organs, and indicates, according to this author, that the auxin is produced in the tip. The concentration of the auxin within the first leaf is ten times that of the coleoptile tip (Thimann and Skoog 1940).

¹ This study was made at Connecticut College for Women, New London, Connecticut. The author expresses appreciation to Dr. George S. Avery, Jr., for making possible this investigation and for helpful criticism during the preparation of the manuscript.

The endosperms of germinating seedlings of *Avena* contain no ascorbic acid (Clark 1937). The coleoptiles of the same seedlings contain 0.54 mg./gm. fresh weight. Ascorbic acid is formed in the coleoptile, accumulating in the tip more than in other parts. This may mean that synthesis occurs at the tip, as is true of auxin. The precursor of ascorbic acid is probably moved from the seed and made active at the tip of the coleoptile.

Peptidase determinations were made on segments of *Avena* coleoptiles of various ages by Avery and Linderstrøm-Lang (1940). Peptidase activity, reduced weight, and cell number, when measured per segment, were found to decrease in progressively older coleoptiles. For any given coleoptile of 4 mm. or more in length, enzyme activity per unit weight of tissue or per cell is consistently greater at the tip.

A considerable amount of evidence concerning the occurrence and distribution of physiologically active substances in the *Avena* seedling, particularly in the coleoptile, has accumulated. Also there is a considerable amount of knowledge concerning the cellular behavior in these seedlings. The exact relationship between these physiologically active substances and cell division, cell enlargement, and differentiation remains to be determined.

MATERIALS AND METHODS

Victory oats (*Avena sativa* var. "Victory," obtained from Mr. Marshall Rumsey, Batavia, N. Y.) were grown on moist filter paper in large Petri dishes or culture dishes. These were placed in a dark room where temperature and relative humidity were maintained at 25° C and 88–90 per cent. One set of seedlings was exposed to greenhouse conditions during the day.

At daily intervals whole seedlings were harvested, counted, and dried in an oven at 70° C for 12 hours. Other plants were harvested, counted, and each divided into four parts: (1) endosperm, (2) coleoptile, (3) leaves, and (4) root system plus the first internode. After harvest separate organs were desiccated in the same manner as the entire seedlings. All material was preserved in the dry state over calcium chloride in a desiccator until the assays could be made. The material was ground fine in a glass mortar and extracts were made. For entire seedlings and the endosperms of various stages, 0.5 gm. samples were used. Each sample was autoclaved in 20 ml. of 1 N H₂SO₄ and the final volume of each extract was 30 ml. Glass-distilled water was used throughout, and the glassware was cleaned with chromic acid or calgonite solution, washed thoroughly, and rinsed in distilled water. The work was performed with the aid of filtered red light until the riboflavin determinations were completed.

Thiamine activity was determined by the *Phycomyces* assay method, as described by Bonner and Erickson (1938). Riboflavin and niacin were determined by the microbiological tests involving the use of *Lactobacillus casei*

and *Lactobacillus arabinosus* as described by Snell and Strong (1939) and Snell and Wright (1941). Thiamine tests were made in triplicate at one concentration level. Duplicate tests at each of four concentration levels were made for riboflavin and niacin. The amounts of extracts to be used were determined by preliminary trials and appropriate aliquots were selected, so that growth of the indicator organism would fall within a suitable range of response. The data are expressed as micrograms per gram of dry matter.

RESULTS

Seeds and Seedlings. Entire embryos were removed from one-day-old seedlings and the embryos and endosperms assayed separately. The ratio of the dry weight of the endosperm to the embryo is approximately one to fifteen. Assays revealed that the embryos at this stage of development contain, per gram dry weight, approximately 8 times the amount of thiamine, 7 times the amount of riboflavin, and 12 times the amount of niacin found in the endosperm. Per seedling, the embryo contains approximately 50 per cent as much thiamine and riboflavin and 80 per cent as much niacin as the endosperm.

To determine whether the high content of vitamins in the one-day-old embryos was due to a release or change of precursor into active form, brought about by soaking, unsoaked seeds and seeds from which the embryo had been removed were assayed. In removing the embryos from the dry seeds some portions of the endosperm were scraped away. Assays indicated that there is little or no change in the distribution of thiamine, riboflavin, and niacin in the embryo and endosperm during the first day of germination. A comparison of the assays of entire unsoaked seeds with one-day-old seedlings shows little if any change in thiamine content, approximately 10 per cent increase in riboflavin, and about 30 per cent increase in niacin.

The average dry weight of the seedlings decreased from about 23 mg. to 14.5 mg. during the 7 days' growth in the dark (fig. 1). Per dry weight the thiamine showed a slight increase, but this was only an apparent increase, since the dry weight decreases during germination. When the thiamine content is calculated per seedling it is evident that there is little if any change. The riboflavin and niacin reached the maximum value after five days' growth in the dark. Riboflavin increases approximately 13-fold per unit dry weight but only 8-fold per seedling. The most rapid increase in riboflavin occurs from the second to the fifth days. The apparent increase in niacin calculated per dry weight is nearly 9-fold but the actual increase is about 5.5 times. Niacin increases most rapidly during the first three days of germination.

A set of seedlings grown simultaneously with those just discussed, but exposed to greenhouse conditions during the day, was assayed after five

days' growth. The results agree with those obtained from plants of the same age grown in the dark, except that the riboflavin values are much lower.

Endosperm. During the seven-day period of growth the dry weight of the endosperm decreased from approximately 20 mg. to 2 mg. When calcu-

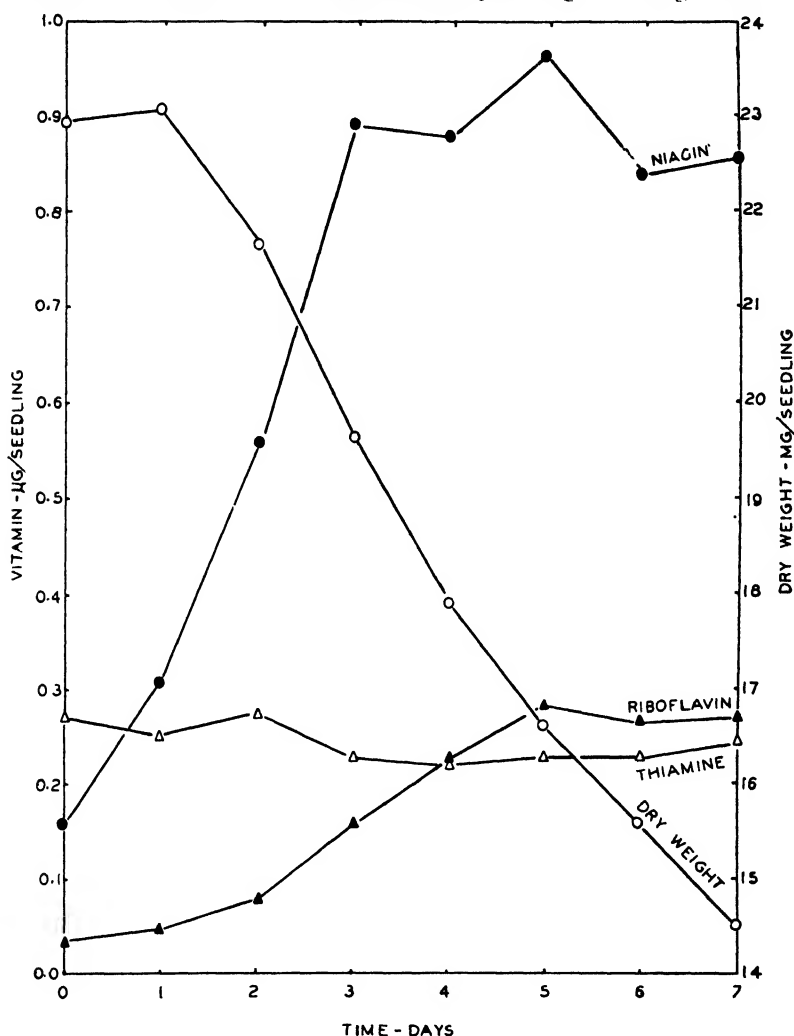
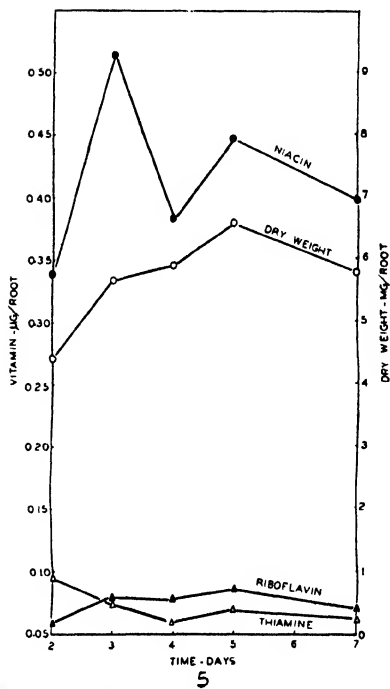
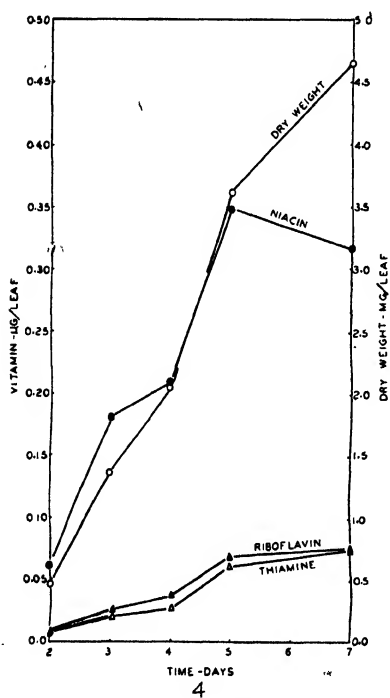
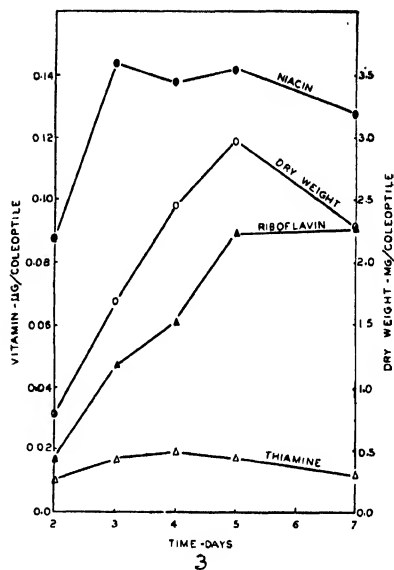
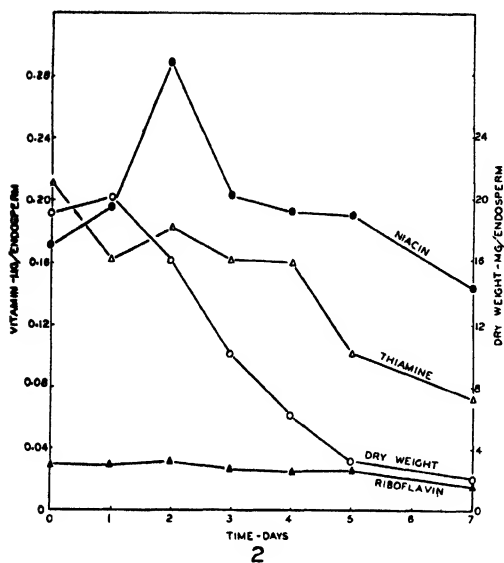


FIG. 1. Thiamine, niacin, riboflavin, and dry weight per seed and seedling of *Avena* grown for different lengths of time on moist filter paper in Petri dishes. Per seedling the riboflavin and niacin content increase during germination while the thiamine content remains nearly constant.

lated per gram dry weight, the three vitamins show considerable increases, but actually the stores of vitamins as well as food materials in the endosperm are depleted as the embryo develops (fig. 2). The riboflavin content of the



Thiamine, niacin, riboflavin, and dry weight of organs of *Avena* seedlings at successive stages in germination. FIG. 2. Endosperm. FIG. 3. Coleoptile. FIG. 4. Leaf. FIG. 5. Root.

endosperm is very low and changes very little during the 7 days' growth period; the greatest decrease occurs between the fifth and seventh days. The thiamine content falls off most rapidly between the fourth and seventh days. The niacin content increases rapidly during the first two days and then decreases at about the same rate. This initial increase is probably the result of the change of some precursor into an active form.

Coleoptile. The dry weight of the coleoptile increases from the second to the fifth day and then decreases (fig. 3). Per coleoptile thiamine increases slightly from the second to the fourth day and then decreases slowly. The riboflavin content per organ more or less parallels the change in dry weight during the first five days. The greatest increase in niacin occurs during the first three days.

Leaf. From the second to the seventh day the thiamine, riboflavin, and niacin content per leaf increases approximately 9-fold, 10-fold, and 7-fold respectively (fig. 4). During this period the dry weight increases about 10 times. Since the dry weight is increasing as fast or faster than the vitamins they appear to change little or decrease if calculated per unit dry weight.

Roots. The data for the roots over three days old are of questionable validity. Roots grown on moist filter paper are developing under very abnormal conditions and after about three days become so entangled in the paper that it is difficult to separate them. Riboflavin and niacin increase slightly per root during the early period of growth while the thiamine content decreases (fig. 5).

DISCUSSION

Since thiamine, riboflavin, and niacin function as parts of respiratory enzyme systems, it is not surprising that embryos contain rather large stores of them. Their role is one of making available to the young plant building materials stored in the endosperm. Ward (1943) has investigated the distribution of thiamine in the wheat grain. He reports that the cotyledon and epithelial layers are the centers of high thiamine concentration within the wheat kernel. One might expect the same distribution within the *Avena* seed.

As the seedling grows the vitamins are constantly being used. The assays do not indicate the total amounts of vitamins produced within the seedling but rather the excess of production over the amounts used.

The data suggest the leaves of *Avena* as centers of vitamin synthesis rather than the roots. During the growth period under consideration the leaves increase in each of the three vitamins. Assays of plants grown in soil under normal conditions should be made to supplement these studies.

SUMMARY

Avena seedlings, growing in the dark, make significant increases in riboflavin and niacin during the first five days of germination. There is little or no change in the thiamine content.

Approximately 50 per cent as much thiamine and riboflavin and 80 per cent as much niacin are contained in the embryo of an *Avena* seed as in the endosperm: the dry weight of the embryo is about 1/15 that of the endosperm.

With the decrease in dry weight of the endosperm during germination, thiamine and niacin per organ decrease also; the riboflavin content remains low. The leaf shows absolute increases in these three vitamins during the five-day period. The coleoptile increases in riboflavin throughout its period of growth, although its niacin content increases only during the first three days. The thiamine content of the coleoptile shows little or no change during germination.

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THE GENUS *CNIDOSCOLUS*: GENERIC LIMITS AND INTRAGENERIC GROUPS

ROGERS McVAUGH

The genus *Cnidoscolus* (Euphorbiaceae) is a remarkably homogeneous, strictly American group of perhaps 40 or 50 species, and is evidently a natural unit from the evolutionary standpoint. In recent years it has often been merged with *Jatropha*, perhaps chiefly because of the influence of Mueller Argoviensis, who treated it as a section of *Jatropha* in the *Prodomus* of de Candolle (1866) and in the *Flora brasiliensis* (1874). Actually the characters of *Cnidoscolus* are such as to separate it readily from *Jatropha* proper; the line of demarcation between the two is quite as clear if not more so than that between *Jatropha* and *Manihot*, *Jatropha* and *Aleurites*, or even *Jatropha* and *Hevea*. When judged by the criteria used for the delimitation of genera in the Euphorbiaceae generally, *Cnidoscolus* seems unquestionably to merit consideration as an independent genus characterized by the possession of a single white floral envelope, stinging epidermal hairs, and distinctive petiolar glands.

The species of *Jatropha*, in the restricted sense, regularly have two well-differentiated floral envelopes, and are destitute of stinging hairs. Glands of the *Cnidoscolus* types (at the summit of the petiole) appear to be entirely wanting in *Jatropha*. The pith in *Cnidoscolus* is characteristically white, and proportionately large, divided into thin transverse plates, while in *Jatropha* the pith is usually relatively small and solid. In *Cnidoscolus* the styles are repeatedly dichotomous (3 to 5 times) and terminate in very slender tips, while those of most species of *Jatropha* are once-forked and terminate in fleshy capitate or hooded stigmas. In *Cnidoscolus* the development of rudimentary stamens in the pistillate flowers and filiform "staminodia" in the staminate flowers is the rule in most species, while these structures are met with but infrequently in *Jatropha* proper. In most species of *Cnidoscolus* the annular gland on the staminal column is raised noticeably above the base of that column, but it is sessile in those (relatively few) species of *Jatropha* having an annular gland rather than five discrete glands.

Before passing to a consideration of the groups within *Cnidoscolus*, it is necessary to discuss the typification of the genus *Jatropha* which, as originally proposed by Linnaeus in 1753 and 1754, included two species now referred to *Cnidoscolus*, one species subsequently segregated as the type of the genus *Manihot*, one species now commonly regarded as an *Aleurites*, and three species that are still widely known as *Jatropha gossypifolia*, *Jatropha multifida*, and *Jatropha Curcas*. It is evident that stability in present-day

generic nomenclature in these groups depends upon the determination of the type-species of *Jatropha* and, luckily for such stability as may now exist, there seems to be sufficient ground for the designation of *J. gossypifolia* L. as the type of the genus.

Jatropha gossypifolia (Sp. Pl. 1006. 1753) was based by Linnaeus upon plates and descriptions of Sloane, Commelin, Bauhin, and Royen and, alone among the species of *Jatropha* published at this time, it was characterized by a detailed and reasonably accurate twelve-line description attributed to Royen. This description, almost verbatim, forms the basis of the generic description of *Jatropha* in the *Genera plantarum* of 1754, the only significant additions to the generic character at this time being mention of the staminate corolla as "monopetala, hypocrateriformis. *Tubus* brevissimus," and brief mentions of the calyces. Of the staminate flowers Linnaeus said: "CAL. Perianthium vix manifestum," and of the pistillate: "CAL. nullus."

These references to the calyx have been used by Mackenzie (1929), in an attempt to show that *Jatropha Manihot* L. must be regarded as the type of the genus. In conclusion Mackenzie says:

"His [Linnaeus'] description calling for but one well-developed floral envelope was evidently based on the first plate (Tournefort 438) cited by him, to which it entirely applies.

"... the original generic description of Linnaeus was based solely on *Jatropha Manihot* L. and it is the only one of his seven species which agrees with his generic description. It in consequence must be taken as the type of the genus."

Although Mackenzie may have been correct in assuming that Linnaeus' description of the calyx was based on Tournefort's plate (which indeed represented a *Manihot* flower with one floral envelope only), it may be pointed out that the description applies equally well either to *Jatropha herbacea* L. or to *J. urens* L., and the latter was specifically mentioned by Linnaeus in a footnote¹ to his generic description, so could hardly have been omitted from his consideration in his compilation of the characters.

In stating that "the original generic description of Linnaeus was based solely on *Jatropha Manihot*," Mackenzie seems to have overlooked the fact that Linnaeus cited in the generic synonymy not only Tournefort's plate, but also a plate from Dillenius' *Hortus elthamensis* (no. 173, representing *J. multifida* L.), and a reference to Houstoun's genus *Jussievia* (that is, to *J. herbacea* L.). If it be again remembered that most of the generic description was taken from that of *J. gossypifolia*, then it is clear that five of the original seven species of *Jatropha* (all except *J. Curcas* and *J. moluccana*)

¹ "OBS. *J. Urens* Stamina novem, erecta, quorum Tria interiora reliquis longiora, quibus (tribus) setae totidem respondent, singulae singulo filamento prope basin insertae." (Gen. Pl. 437. 1754.)

are mentioned or described directly or by implication in the original description.

Hitchcock and Green, in their *Species lectotypicae propositae* (1935), have undertaken to typify the genus *Jatropha* by the species *J. Curcas* L. There seems to be no particular reason for this unless it be that *J. Curcas* is now widespread and familiar in all tropical regions; and the choice of *J. Curcas* as type species would seem an unfortunate one, chiefly because Adanson, in 1763 (Fam. Pl. 2: 356) segregated *J. Curcas* as the type- and only species of a new genus, *Curcas*. *Curcas* has never been widely accepted as a valid genus distinct from *Jatropha*, but its eventual recognition as such would necessitate the renaming of many species now referred to *Jatropha*, if *J. Curcas* were to be considered as the type-species of the latter genus.

For the reasons given above it seems best to regard *Jatropha gossypifolia* L. as the type of the genus. It has not, to my knowledge, been made the type-species of any segregate genus, and the type-specimen, according to Fawcett and Rendle (Fl. Jam. 4: 312. 1920) is preserved in the Linnaean Herbarium. The remaining generic elements comprising the inclusive Linnaean *Jatropha* are then to be referred to *Manihot*, *Aleurites*, and *Cnidoscolus*, as mentioned above. Neither of the two Linnaean species now referred to *Cnidoscolus* could logically be regarded as the type species of *Jatropha*, for *J. urens* is specifically mentioned as constituting an exception to the generic character, and either *J. urens* or *J. herbacea* is excluded by any of several characters or by a combination of these: "COR. [masc.] *Tubus* brevissimus"; "Filamenta . . . in medio approximata"; "COR. [fem.] pentapetala, rosacea"; "Styli . . . dichotomi. *Stigmata* simplicia."

It remains but to establish the correct name for the segregate genus including *Jatropha urens* and *J. herbacea* L., and this has been attempted by Wheeler (1939), who has proposed the conservation of the name *Cnidoscolus* Pohl (Pl. Bras. Ic. 1: 56. pl. 49. 1827) over *Jussievia* Houst. (Reliq. 6. pl. 15. 1781) and *Bivonca* Raf. (Specchio delle Sci. 1: 156. 1814). This course appears a most suitable one, for *Cnidoscolus* has been widely known and used since its proposal, while neither *Jussievia* nor *Bivonca* has been accepted by any considerable group of workers.

Cnidoscolus has been variously divided into subgeneric groups. Mueller [in Linnaea 34: 210-212. 1865, and (in brackets below) in DC. Prodr. 15(2): 1096-1102. 1866] proposed to divide *Cnidoscolus* (which he considered a section under *Jatropha*) into the subsections *Eucnidoscolus* and *Calyptosolen*, which he distinguished as follows:

1. Calyx foemineus 5-partitus [laciniae segregatim deciduae] *Eucnidoscolus*.
1. Calyx foemineus 5-fidus, inferne tubulosus, mox basi circumscisso-liber ovariumque calyptratim tegens [dein inferne integer v. lateraliter ruptus.—
Habitus omnino cum subseccione *Eucnidoscolo* quadrans] *Calyptosolen*.

It seems clear from Mueller's Latin that in his mind the distinction between these subsections lay in the degree of coherence of the calyx-segments of the pistillate flower. His subsection *Calyptrosolen* included but two species, *J. Liebmanni* Muell. Arg. and *J. tubulosa* Muell. Arg., and photographs of the type material of these species show the character to which he referred: the calyx of the pistillate flower, after anthesis, breaks away from the base as a unit and forms a calyptra-like structure over the ovary until it is ruptured by the growth of the capsule or until the segments (which are often but loosely coherent) separate naturally.

Mueller recognized 16 species of *Cnidoscolus*; Pax, on the other hand, in the *Pflanzenreich* (1910) accepted 44 species, and divided the group (which he understood as a subgenus) into six sections based primarily upon characters of the androecia. In Pax's treatment the sections *Vitifoliae* and *Hamosae* together comprised 19 species, native to temperate and subtropical South America, having the stamens 15-30 in number and in 3-6 whorls on the staminal column. The section *Oligandrae* comprised three South-Brazilian species having 6-8 irregularly disposed stamens, and the section *Platyandrae* included a single anomalous Cuban species; the remaining 21 species known to Pax, those having the stamens regularly 10 in number and in two whorls on the staminal column, were assigned to section *Jussieuia* or to *Calyptrosolen*. In circumscribing *Calyptrosolen* Pax seems to have misinterpreted the character as set forth by Mueller, for in his key to *Jatropha* (op. cit., 23) he distinguished *Jussieuia* and *Calyptrosolen* as follows:

- | | |
|--|------------------------|
| 1. Calyx ♀ caducus | <i>Jussieuia</i> . |
| 1. Calyx ♀ basi disciformiter persistens | <i>Calyptrosolen</i> . |

This idea of a persistent basal calyx-disk under the ovary was repeated by Pax in his descriptions of individual species of *Calyptrosolen* and was evidently the principal criterion upon which he based the section; although he repeated Mueller's character of the tubular calyx ("Calyx ♀ 5-lobus, inferne tubulosus, mox basi circumscisso-liber et ovarium calyptratim tegens . . ."), he seems to have attached little importance to it, for the opposing character is never emphasized or even definitely stated for the contrasted section *Jussieuia*.

About three-quarters of the species having biverticillate stamens (*Jussieuia* and *Calyptrosolen* of Pax) occur in the Mexican-Central-American region, and the two groups were keyed out by Standley (Contr. U. S. Nat. Herb. 23: 634. 1923) as follows:

- | |
|---|
| 1. Pistillate calyx persistent as a disk at the base of the capsule |
| 1. Pistillate calyx caducous |

It seems necessary to point out here that *Calyptrosolen* was delimited by Pax on the basis of an exceedingly variable and often imagined character which is

of no value whatever in separating taxonomic groups. In *Cnidoscolus* the pistillate calyx is deciduous after anthesis in all species, either as 5 distinct lobes or as a tubular unit, and the tissues persistent at the base of the flower may take the form of a narrow rim encircling the peduncle and the scar left by the fallen calyx, or the form of five small projections alternating with the scars of the calyx-lobes. These persistent tissues vary in size from one individual to another in the same species, but I have not been able to establish any correlation between a tubular calyx (the character of *Calyptrosolen* as understood by Mueller) and the persistence of an enlarged basal disk (the character as understood by Pax); it is impossible to determine the tubular or non-tubular character of the deciduous part of the calyx by examination of the persistent basal part after the disappearance of the floral envelope. A few species, notably *Jatropha urnigera* Pax, *J. Löfgreni* Pax & Hoffm., and *J. tenuifolia* Pax & Hoffm., all South American species described from single collections, are stated to have distinct cupuliform disks; authentic material of these has not been available for study, but no species known to me can be distinguished by the presence of such disks from the species assigned by Pax to *Jussieuia*.

The most recent work on the taxonomy of *Cnidoscolus* is that of Brother León, who has recently (1938, 1941) proposed the segregation, under the name *Victorinia*, of the West Indian species said to have 15 stamens, 5 carpels, a seed lacking a caruncle, and a fleshy fruit with a delicate endocarp adherent to the seed. The wisdom of such segregation is of course, partly a matter of opinion, but until the West Indian species are better known, and their genetical constituents and limits of variation more fully studied, they are probably best regarded as members of *Cnidoscolus*. Their staminal complement and general morphology show them to be akin to the South American members of *Eucnidoscolus*, from which they differ in characters of the fruit only. The possession of 5 (rather than 3) carpels is in itself insufficient to justify generic segregation, and the characters of the small caruncle and delicate endocarp are likewise rather tenuous; there is evidently an evolutionary connection between these species and the pinnately veined South American ones, but its strength must remain to be demonstrated.

The following conclusions are based chiefly upon the material in the United States National Herbarium and that in the Herbarium of the National Arboretum; certain material at the New York Botanical Garden, the Gray Herbarium and the Arnold Arboretum has also been examined, and I am grateful to those in charge of these herbaria for the many courtesies they have extended.

Most of the known species of *Cnidoscolus* are readily assigned to definite sectional and subsectional groups, as follows:

1. Petiolar glands normally present, solitary or paired at the summit of the petiole; leaves palmately veined; stamens usually 10 (7-10), all monadelphous, the filaments 2-verticillate; species mostly North American Sect. *Calyptrosolen*.

1. Petiolar glands, if present,² usually several, finger-like, papilliform or filiform, at base of blade; venation various; stamens various 2.
2. At least the outer whorl of filaments distinct to the base or essentially so (stamens 10 in all); glands (probably always present) papilliform; leaves palmately veined and lobed Sect. *Jussiauia* 3.
3. Filaments all distinct; one Brazilian species Subsect. *Urnigerac.*
3. Inner whorl of filaments monadelphous, coherent into a column. Subsect. *Urentes.*
2. Stamens all monadelphous, 8-15 or more; glands present or absent 4.
4. Petiolar glands several, 1.5-3 mm. long, elongate-filiform, the glandular tissue distal; leaves palmately veined; filaments 10, 2-verticillate; Yucatán *Cnidoscolus Souzae.*
4. Petiolar glands several (minute and papilliform) or wanting; leaves palmately or pinnately veined; South America or Greater Antilles 5.
5. Leaves pinnately veined; petiolar glands [usually] wanting. Sect. *Cnidoscolus* 6.
6. Stamens 10, 2-verticillate; carpels 3 Subsect. *Phylacanthac.*
6. Stamens 15-20, 3- to 4-verticillate or irregularly inserted; carpels 3 or 5 (6) 7.
7. Stamens 3- to 4-verticillate; carpels 3; endocarp hard; central subtropical South America Subsect. *Eucnidoscolus.*
7. Stamens about 15, clustered (not verticillate) on the column; carpels 5; endocarp delicate; Cuba and Hispaniola. Subsect. *Victorinia.*
5. Leaves palmately veined 8.
8. Blades deeply or shallowly 3- to 5-lobed; petiolar glands several, small, papilliform; stamens 15-20 (28), 3- to 6-verticillate; subtropical South America Sect. *Vitifoliar.*
8. Blades compound or essentially so, divided to the base into 10 or fewer irregular elongate lobes; petiolar glands unknown; stamens 8-10, 2-verticillate; Cuba Sect. *Platyandrac.*

1. Sect. **Cnidoscolus** (Muell. Arg. emend. McVaugh) McVaugh,
comb. nov.

Jatropha, sect. *Cnidoscolus* Muell. Arg. *Linnæa* 34: 210. 1865.

Jatropha, sect. *Cnidoscolus*, subsect. *Eucnidoscolus* Muell. Arg. l. c.

Jatropha, sect. *Eucnidoscolus* Muell. Arg. ex Pax, *Natürl. Pflanzenfam.* 3^o: 75. 1890.

It appears that according to a strict interpretation of the rules of nomenclature (Art. 58), the name *Cnidoscolus* must be retained for some part of the genus of the same name, since it is the earliest sectional name available. It seems proper to apply it to that section which includes the type-species of Pohl's genus, *Cnidoscolus hamosus* (*C. hamosus* is certainly a suitable choice for type-species; the original material was collected by Pohl himself and was well described and figured, the first species so treated; it was designated as type-species by Small (in Britton & Brown, *Ill. Fl.* ed. 2, 2: 462. 1913) and there seems no reason to disagree with this choice). I am therefore restrict-

² If absent, then the anthers 10 and the outer filaments distinct to the base, or the anthers 15 or more, or the leaves pinnately veined or (in 2 Cuban species) palmately compound.

ing the application of Mueller's name *Cnidoscolus*, when used in the sectional category, to those species having pinnately veined and mostly eglandular leaves, reduced and few-flowered inflorescences, and mostly numerous (15 or more) stamens, typified by *C. hamosus*.

1a. Subsect. **Victorinia** (León) McVaugh, comb. nov.

Victorinia León, Mem. Soc. Cub. Hist. Nat. 15: 242. Jl 10, 1941.

Jatropha, sect. *Acrandrae* Urb. Symb. Ant. 7: 516, nomen. 1913.

Cnidoscolus, sect. *Acrandrae* Pax & Hoffm. Natürl. Pflanzenfam. ed. 2. 19c: 167. 1931.

TYPE-SPECIES, *Victorinia regina* (León) León, selected by Brother León (l.c.) as the type of his genus. Two Antillean species: *C. acrandrus* (Urb.) Pax & Hoffm.,³ described from the province of Barahona, República Dominicana, and *Jatropha* (*Victorinia*) *regina* León, of the Province of Oriente, Cuba. This latter species, from the description, is not very different from *C. acrandrus*, and until the two are thoroughly compared it seems unwise to make the new combination required in *Cnidoscolus*. The differences, as summarized by Brother León (1941, p. 243), are in the slightly larger and relatively narrower fruits of *C. acrandrus*, and in the leaves, which in *C. acrandrus* are said to be larger, more oval, with narrower and rounder base and less spreading nerves than in *J. regina*. For remarks on the taxonomy of this group see above.

1b. Subsect. **Eucnidoscolus** (Muell. Arg. emend. McVaugh)
McVaugh, comb. nov.

Jatropha, sect. *Cnidoscolus*, subsect. *Eucnidoscolus* Muell. Arg. Linnaea 34: 210. 1865.

Jatropha, sect. *Vitifoliae*, subsect. *Loasiformes* Pax, Pflanzenreich IV. 147: 92. 1910.

Jatropha, sect. *Hamosae* Pax, op. cit., 94.

Cnidoscolus, sect. *Vitifoliae*, subsect. *Loasiformes* (Pax) Pax & Hoffm. Natürl. Pflanzenfam. ed 2. 19c: 164. 1931.

Cnidoscolus, sect. *Hamosae* (Pax) Pax & Hoffm., l. c.

TYPE-SPECIES, *Cnidoscolus hamosus* Pohl. A small subsection of interior South America, comprising about 9 described species with leaves unlobed or somewhat pinnately lobed, depauperate cymes of 1–10 flowers each, and the

³ In the second edition of *Die Natürlichen Pflanzenfamilien*, Pax and Hoffman (1931) introduced into literature about 25 new names in *Cnidoscolus*, all of which are transfers based on previously described species of *Jatropha*. Technically perhaps none of these is a valid transfer, for in no case do the authors cite the original place of publication or the name-bringing synonym. For species of *Jatropha* previously described by Pax alone or by Pax & Hoffmann, they customarily cite no parenthetical authority, apparently assuming that such a practice would make for redundancy. Because of the very formal treatment of *Cnidoscolus* in the work in which these "transfers" appear, the division of the genus into sections based on those earlier proposed by Pax in the *Pflanzenreich*, and the systematic enumeration of the species in the same order in the two publications, there can be no reasonable doubt of the source of any of the names proposed in *Cnidoscolus*, especially since for each section (thus presumably also for the included species) a specific reference to the *Pflanzenreich* is given; this seems to comply with the letter of Art. 44, which requires the "citation of a previously and effectively published description."

sepals of the pistillate flowers, where known, distinct. Mueller's subsection is to be restricted so as to include but these species, excluding all the species known to him in 1865-6 except *Jatropha obtusifolia* and *J. hamosa*.

1c. Subsect. **Phyllacanthae** (Pax) McVaugh, comb. nov.

Jatropha, sect. *Jussievia*, subsect. *Phyllacanthae* Pax, Pflanzenreich IV. 147: 96. 1910.

Cnidoscolus, sect. *Jussievia*, subsect. *Phyllacanthae* (Pax) Pax & Hoffm. Natürl. Pflanzenfam. ed. 2. 19c: 165. 1931.

TYPE-SPECIES: The type-species of Pax's original subsection can be nothing but *Jatropha phyllacantha* Muell. Arg., the only species included. This name, however, is untenable, being merely a herbarium name taken up by Mueller to include three species previously proposed by Pohl, and the species must take one of the names proposed by Pohl for what Mueller considered to be varieties of the same plant. The inclusive species may be called by the appropriate name *Cnidoscolus quercifolius* Pohl, and the names *Cnidoscolus lobatus* Pohl, *C. repandus* Pohl, and *Jatropha phyllacantha* Muell. Arg. should be relegated to the synonymy of *C. quercifolius*.

The two known species of this subsection, *C. bellator* (Ekm. ex Urb.) León, of western Cuba, and *C. quercifolius* of southeastern Brazil, are anomalous in this section because of the biverticillate anthers. Mueller states, however (1866, p. 1098), that the sterile filaments of *C. quercifolius* may bear rudimentary anthers, and if true this doubtless emphasizes the relation between it and those species with 3-verticillate stamens.

2. Sect. **PLATYANDRAE** (Pax) Pax & Hoffm. Natürl. Pflanzenfam.
ed. 2. 19c: 166. 1931.

Jatropha, sect. *Platyandrae* Pax, Pflanzenreich IV. 147: 110. 1910.

TYPE-SPECIES: **Cnidoscolus Rangel** (Gomez) McVaugh, comb. nov. *Jatropha peltata* C. Wright in Sauv. Anal. Acad. Ci. Habana 7: 155. 1870, non *J. peltata* Sessé in Cerv. Supl. Gac. Lit. Mex. 3. 2 Jl 1794, nec *J. peltata* H.B.K. Nov. Gen. & Sp. 2: 104. 1817, nec *J. peltata* Wight, Ic. pl. 1169. 1850; *Jatropha Rangel* Gomez de la Maza, Anal. Hist. Nat. Madrid 23: 51. 1894; *Jatropha platyandra* Pax, Pflanzenreich IV. 147: 110. 1910; *Cnidoscolus platyandrus* I. M. Johnst. Contr. Gray Herb. 68: 86. 1923. The section is apparently endemic in Cuba, comprising only the type-species and *C. Matosii* León, which is said to have 8 stamens and to differ from *C. Rangel* in minor particulars.

Pax (1910, l.c.) attached considerable taxonomic importance to a single character in *C. Rangel*, that of a relatively broad connective in the anther; Brother León (1938, 1941) attaches little importance to this, either in *C. Rangel* or in other species, considering that the connective is distorted by drying and alternate boiling and redrying. Almost no material of this section is available for study, but it seems to be quite distinct from all the other

sections, apparently being the end-result of the development of some insular progenitor of *Cnidoscolus*.

3. Sect. *CALYPTROSOLEN* (Muell. Arg. ex Pax) Pax & Hoffm. Natürl. Pflanzenfam. ed. 2. 19c: 165, emend. McVaugh. 1931.

Jatropha, sect. *Cnidoscolus*, subsect. *Calyptrosolen* Muell. Arg. Linnaea 34: 212. 1865.

Jatropha, sect. *Calyptrosolen* Muell. Arg. ex Pax, Natürl. Pflanzenfam. 3^a: 75. 1890.

Jatropha, sect. *Jussieuta* (Houst.) Pax, Pflanzenreich IV. 147: 96, pars. 1910.

Jatropha, sect. *Oligandrae* Pax, op. cit., 109.

Cnidoscolus, sect. *Oligandrae* (Pax) Pax & Hoffm. Natürl. Pflanzenfam. ed. 2. 19c: 166. 1931.

TYPE-SPECIES, *Jatropha tubulosa* Muell. Arg. Mueller's subsection included two species only, *Jatropha Liebmanni* Muell. Arg., and *J. tubulosa*, and the section as technically validated by Pax in 1890 included but the same two species. As thus constituted the group depended upon a single character, the coherence of the pistillate calyx into a tube. As this character seems not to be a particularly fundamental one in *Cnidoscolus*, and indeed varies to some extent even within single species, it seems proper to depend rather upon the combination of characters by which these species are obviously related to others in the same geographical area, and to enlarge the section to include all those species having palmately lobed leaves with large single or paired petiolar glands, monadelphous 2-verticillate stamens, and relatively floriferous cymes. As thus constituted the section appears to be very homogeneous, scarcely to be divided, and including perhaps 20 species in the Mexican-Caribbean region, with some few additional species in Paraguay and south-eastern Brazil; the *Oligandrae* of Pax appear to belong here on the basis of the 2-verticillate stamens, the ample cymes and the petiole "apice supra glanduloso-incrassatus" (Pax 1910), but it may be that the *Oligandrae* comprise but a single species, *C. oligandrus* (Muell. Arg.) Pax. *Jatropha pyrophora* Pax, described from a single collection from northern Peru, also appears, from description and a photograph (Field Mus. neg. 5400) of the type to belong to this section; *J. jaenensis* Pax & Hoffm., based on Weberbauer's no. 6234, is from the same general region and may belong here also.

The Mexican and Central American species of this section have recently been treated at some length (McVaugh 1943); the following additions are necessary:

Cnidoscolus Kunthianus (Muell. Arg.) Pax & Hoffman. was based chiefly upon a Bonpland specimen from Cumana, Venezuela, which is to be regarded as the type; I do not know the identity of this species, but Mexican specimens referred to it are *C. multilobus* (Pax) Johnst. or *C. tubulosus* (Muell. Arg.) Johnst., and *C. Kunthianus*, whatever its identity, is doubtless to be excluded from the Mexican flora.

Cnidoscolus fragrans (H.B.K.) Pohl, and *C. quinquelobatus* (Mill.) León, both supposed to have come from Cuba, are imperfectly known; the

types of both were examined by Mueller, and from his descriptions it seems certain that both belong to this section, but their actual origin is unknown, as pointed out by Brother León (1938): "*J. fragrans* y *J. quinquelobata* . . . no han sido encontradas por los botánicos modernos; lo cierto es que en la actualidad no existen cerca de la Habana ni de Regla [their respective type-localities]."

Cnidoscolus rotundifolius (Muell. Arg.) McVaugh, comb. nov. *Jatropha rotundifolia* Muell. Arg. *Linnaea* **34**: 211. 1865; *Cnidoscolus inermiflorus* I. M. Johnst. Contr. Gray Herb. **68**: 85. 1923. The type-locality of *J. rotundifolia* is "In Mexici prov. San Luis," and a photograph (Field Mus. neg. 7170) of the type collection, *Virlet d'Aoust 147*, shows clearly that the species is identical with *C. inermiflorus*, which is based on *Edward Palmer 140* (of 1907), and of which I have seen the type in the Gray Herbarium. The species has not been collected in modern times in the State of San Luis Potosí, but it is well known in the neighboring mountains of Tamaulipas, and, as *Virlet d'Aoust* is known to have collected as far northeast as Valle de Maíz, it is not unlikely that his type material may have come from that general region.

Cnidoscolus tepiquensis (Cost. & Gall.) McVaugh, comb. nov. *Jatropha tepiquensis* Cost. & Gall. Rev. Gen. Bot. **18**: 391. 1906.

Cnidoscolus chayamansa McVaugh, sp. nov.; frutex succulentus subinermis; folia glabra, limbis saepe latioribus quam longioribus, trilobis, lobis flabellatis, in sicco saepe imbricatis; petioli succulenti, quam limbi saepe breviores; glandulae petioli lentiformes, usque ad 1.5 mm. longae; flores foeminei 8–10 mm. longi, calycibus fere ad basin divis; antherae biverticillatae; fructus ignotus.

JATROPHA URENS var. **INERMIS** Calvino, Rev. Agr. Com. y Trab. [Cuba] **2**: 364. Aug. 1919; Skeels in Off. For. Seed & Pl. Intr. Inventory **57**: 43. 1922.

A succulent nearly glabrous shrub up to about 2 m. high, the branches soft, up to about 1 cm. in diameter near the tips; pith large, white, in transverse plates. Stinging hairs none or few. Leaves broader than long (often as 16/13 or 10/8), three-lobed well below the middle, the lobes flabellate, 1–2.5 cm. wide at base, the central lobe 5–8 (15) cm. wide above the middle, the lateral lobes wider, with two main veins, often divided about $\frac{1}{4}$ their length into two lobes. Petioles fleshy, up to 5 mm. in diameter and 8 (15) cm. long, usually much shorter than the blades. Blades glabrous except for the appressed-hispid margins and a minute puberulence at the summit of the petiole. Glands 2 (or reduced to 1) at the summit of the petiole, ovoid, convex, green and very lustrous, up to 1.5 mm. long, separated by a furrow. Blades broadly truncate-cordate, the main veins (5) fleshy at base, strongly ascending and forming a unilateral cup-like arrangement; when the leaves take this position the lobes are all exposed, but when they are pressed flat the lobes overlap. Blades yellowish-green and slightly lustrous beneath and on the veins above, the rest of the upper surface velvety (not lustrous) green

with a suggestion of blue-green. Stipules about 3 mm. long, ovate, caudate-acuminate 1.5–2 mm., laterally glandular-fimbriate, deciduous when the leaves are very small.

Inflorescence 2–5 cm. across in flower, the peduncle 2–3 mm. in diameter, 10–25 cm. long. Cyme-branches about 3-forked, the pistillate flowers in the basal fork or also in the lowest fork of each branch. Bracts minute, about 1 mm. long or less. Pistillate flowers 8–10 mm. long, divided 7–8 mm. into 5 narrowly elliptic rounded recurved lobes about 3 mm. wide, these minutely puberulent without. Ovary about 3 mm. long, minutely puberulent at anthesis. Styles 3–4 mm. long, shortly coherent at base, each of the 3 branches twice (sometimes thrice) irregularly dichotomous. Gland annular, more or less sessile, about 1.5 mm. in diameter and half as high; staminodia subulate, appressed to the ovary, about 1.5 mm. long. Mature capsules and fruit unknown.

Staminate flowers 6–7 mm. long, minutely puberulent without, greenish (the lobes white on the portions covered in bud), the tube cylindric, 1–1.5 mm. in diameter, expanded distally, 4.5 mm. long from base of flowers to base of lobes. Lobes rounded-ovoid, about 2 mm. wide by 2.5 mm. long, glabrous (like the tube) within, white within (like the tube). Stamens 10, 4.5–5 mm. long; gland annular, not sessile, attached along the distal edge, about 1 mm. across, 0.4 mm. high. Outer filaments attached 0.7–1.1 mm. above the gland, free about 0.7 mm. Column of the inner filaments about 3 mm. long, the filaments free 1 mm., incurved. Staminal column white, with a densely white-pilose band above the gland. "Staminodia" 2 (–3), about 2 mm. long. Inner anthers about 0.7–0.9 mm. long and 0.5 mm. wide; outer anthers similar. Pollen apparently none. "Odor [of flowers] rather faint but unpleasantly suggestive of the fls. of *Sterculia foetida*" (Fairchild).

TYPE: In the United States National Herbarium (no. 1472716), collected by *C. L. Lundell* (no. 494), at Honey Camp, in the coastal region of British Honduras, September 17, 1929. Isotype at the New York Botanical Garden.

Additional material: CUBA: Cultivated at Santiago de las Vegas, *M. Calvino*, December 5, 1918 (USNA; P.I. 46862). FLORIDA: Cultivated at the "Kampong," Coconut Grove, *David Fairchild*, July 14, 1943 (USNA).

The source of Dr. Fairchild's material is unknown, but he says: "My trees here . . . all came from a few cuttings planted about 20 years or so ago"; apparently these cuttings were a part of the stock derived from Plant Introduction no. 46862, made by the Office of Foreign Seed and Plant Introduction (now the Division of Plant Exploration and Introduction) in 1918. P.I. 46862 consisted of cuttings, presented by Dr. Mario Calvino, Director of the Estación Experimental Agronómica at Santiago de las Vegas, Cuba, under the name of *Jatropha urens* var. *incrimis* (Off. For. Seed & Pl. Intr. Inventory 57: 43. May 20, 1922). The material of this plant cultivated in Cuba, according to an article by Dr. Calvino (1919), came originally from Yucatán in April, 1918.

Cnidoscolus chayamansa is the edible "chaya" of Yucatán, and for the following information concerning it I am deeply indebted to Sr. Augusto Pérez Toro, Director of the Instituto Agrícola Henequenero at Mérida, Yuc.

In response to my queries concerning the plant, Sr. Pérez writes on November 11, 1943:

"La Chaya . . . es planta originaria de esta región; existen testimonios en el sentido de que antes de la Conquista los mayas la aprovechaban mucho mas que ahora. Se sigue usando para los mismos fines . . . la chaya, que viene siendo la espinaca indígena. A propósito, el nombre castellanizado 'chaya' se deriva del nombre maya CHAY.

"Hay dos plantas conocidas vulgarmente con ese nombre pero se les diferencia llamando a la especie comestible 'chaya mansa,' y a la otra, que al parecer solamente tiene algunos usos medicinales, se le denomina 'chaya brava.' La chaya mansa es muy ligeramente urticante y la brava lo es en mucho mayor grado. La apariencia exterior de ambas es muy semejante."

No information is available concerning the fruit of this species. Dr. Fairchild states that his trees in Florida have not fruited, to his knowledge, in the approximately 20 years during which he has observed them. In Yucatán, as suggested in Calvino's article of 1919 and recently confirmed by Sr. Pérez, the plant is ordinarily propagated by cuttings, which root easily and require little or no care.

Peculiar interest now attaches to the edible "chaya" because of a recent report that the edible parts, the young leaves and shoots, contain considerable amounts of vitamin "C," which suggests that they may constitute a valuable potential source of food here in the United States and elsewhere.

Technically, *Cnidoscolus chayamansa* appears to be rather closely akin to *C. aconitifolius*. It has no particularly close relationship to *C. urens* which, together with the other species of the *Urentes*, is set well apart by its distinctive characters of androecium and foliar glands. *C. chayamansa* may be distinguished from all other species by its short petioles, by the three overlapping flabellate lobes of the leaf blades, by the paired (not solitary and transverse) petiolar glands, and by the position of the main veins at the base of the blade, which in this species are so strongly ascending as to make the blade attenuate at base and obscure the line of demarcation between blade and petiole.

[3a.] *Species incertae sedis.*

Cnidoscolus Souzae⁴ McVaugh, sp. nov.; herba vel frutex usque ad 2-metralis, ramis petiolis pedunculisque pilis urentibus dense munitis; folia triloba, ad marginem praecipue in sinubus aristulas interdum glanduliferas gerentia; glandulae petioli digitiformes filiformesve, 1.5–3 mm. longae, apicibus glanduligeris; flores foeminei 8–9 mm. longi, calycibus fere ad basim divisis; antherae biverticillatae; filamenta exteriora prope basim columnae staminalis inserta, 0.3–0.8 mm. longa; caruncula 1.5–2.5 mm. lata, haud vel vix cordata, supra hylum sidens.

⁴ Named in honor of Dr. Narciso Souza Novelo, of Mérida, Yucatán, the author of *Plantas melíferas y poliníferas que viven en Yucatán, etc., etc.*, and an enthusiastic collector and student of the flora of his State.

A coarse herb or stout shrub up to about 2 m. high, the branches green, at maturity pale brown, up to about 1 cm. in diameter near the tips, usually thickly covered with stinging hairs and often covered with small knobs (the enlarged bases of these hairs) after the hairs fall; branches glabrous except for the stinging hairs, which are often large and stout, up to 12 mm. long and up to 0.5 mm. in diameter at base. Pith white, in transverse plates. Leaves long-petioled, lobed to the middle or beyond; blades truncate or cordate at base, 10–15 cm. long, 12–20 cm. wide, more or less pilose on both surfaces, at least on the veins, with uniformly distributed soft white sharp hairs up to 1 mm. long, these sometimes so abundant as to whiten the surface and make it velvety to the touch. Lobes and principal veins usually 3, the two basal veins sometimes extending into an additional pair of basal lobes smaller than the other 3; lobes oblong or ovate, sometimes with lateral secondary lobes, usually with more or less serrate margins, the veins of the principal lobes and those of the serrations, if any, ending in capillary (not stinging) spines 2–4 mm. long. Margins between the serrations, especially in the broad rounded sinuses between the principal lobes, more or less beset with stout gland-tipped processes about 1–1.5 mm. long, these terminating small veins. Mature blades devoid of stinging hairs, or with a few scattered along the veins on the upper surface. Petiole 10–15 cm. long, beset its whole length with stinging hairs like those of the branches, the degree of investiture varying considerably from plant to plant. Glands 2–4 at the summit of the petiole, consisting of fingerlike processes 1.5–3 mm. long, enlarged and glandular at tips.

Inflorescences 1 or 2 at the tip of a branch, long-peduncled, beset (except for the ultimate branchlets of the cyme) like the stems and petioles with stout stinging hairs. Peduncle 20–30 cm. long, 2–4 mm. in diameter; cyme-branches usually 3, each about 5-forked (sometimes 6-forked); cyme flat-topped when the pistillate flowers open, 4–5 cm. across, the branches then elongating and becoming 8–12 cm. long and rather strongly ascending. Bracts green, leafy, 1.5–5 mm. long (the lower often 3–5 mm.), pilose like the leaves and smallest branchlets of the cyme. Pistillate flowers borne usually in the basal fork and in the first three forks of each branch, not more than about 10 capsules usually maturing in each inflorescence; capsules often fully mature when the staminate flowers on the same branches open. Pistillate flowers 8–9 mm. long, divided 7–8 mm. into 5 oblong or rounded obtuse spreading lobes 3.5–5 mm. wide, the lobes minutely puberulent, especially near the tips, on both surfaces. Ovary about 2.5 mm. long, sparsely or densely silky-strigose in anthesis, later developing a dense covering of stinging hairs. Styles nearly sessile, about 3 mm. long, irregularly forked 2 or 3 times. Gland annular, about 1 mm. in diameter; staminodia 10, white, bristle-like, about 0.4 mm. long. Staminate flowers 8–10 mm. long, the lobes rounded, spreading, about 3 mm. wide, 3–4 mm. long, the tube campanulate, 5–6 mm. long; whole perianth minutely puberulent without and near the tips of the lobes within. Staminal column 7.5–9.5 mm. long, pilose at base; inner filaments 1.5–2 mm. long, their anthers 1–1.3 mm. long; outer stamens near base of column, the filaments 0.3–0.8 mm. long, the anthers 1.3–1.7 mm. long; “staminodia” 3, 1–2 mm. long; gland annular, about 0.5–0.7 mm. in diameter, about 0.5 mm. above the base of the column. Capsule oval to subglobose, broadly rounded at both ends, green, slightly roughened by the bases of the

stinging hairs, often about 7 mm. in diameter, 8–9 mm. long, stalked about 1 mm. in the persistent lobed base of the perianth. Seeds oblong, somewhat flattened, conspicuously mottled at full maturity, truncate at base, about 4 mm. wide and 7 mm. long; caruncle white or pale yellowish, fleshy, 1.5–2.5 mm. wide, not at all or scarcely cordate, usually standing well above the small hilum.

Specimens examined: BRITISH HONDURAS: Corozal Dist., *Percy H. Gentle* 247 in 1931–32 (NY, US), 332 in 1931–32 (US); San Juquin, Corozal Dist., *Percy H. Gentle* 4983, Sep. 1933 (NY). CAMPECHE: Tuxpeña, *C. L. Lundell* 1189, Jan. 15, 1932 (G, Type; NY, US). YUCATAN: Buena Vista Xbac, *G. F. Gaumer* 1069, Apr. 1895–96 (G, US). Mérida, *N. Souza Novelo* in 1944 (USNA),

A well-marked species, restricted to the Yucatan Peninsula. Although technically excluded from *Calyptrosolen* by the unique petiolar glands, it agrees so well in other ways with the members of that section that I hesitate to assign it to any other group. Its shrubby habit and numerous elongated petiolar glands suggest some relationships to the *Urentes* also. It is easily identified by the leaves alone; no other species is known to have the characteristic almost filiform glands of the petiole, in combination with gland-tipped setae along the leaf-margins. The pistillate flowers may be confused with those of *C. aconitifolius*, but in that species the caruncle is cordate and the foliar glands are solitary and broad.

4. Sect. JUSSIEUIA (Houst.) Pax & Hoffm. Natürl. Pflanzenfam.
ed. 2. 19c: 164. 1931.

Jussievia Houst., Reliq. Houstoun. 6. 1781, as genus.

Jatropha, sect. *Jussievia* (Houst.) Pax, Pflanzenreich IV. 147: 96. 1910.

TYPE-SPECIES, *Jatropha herbacea* L. As here understood this is a small group of herbaceous or shrubby species from which are excluded several members of *Calyptrosolen* placed here by Pax (1910): *C. calyculatus*, *C. quinquelobatus*, *C. angustidens*, *C. aconitifolius*, *C. Kunthianus*, *C. rotundifolius*, and *Jatropha pyrophora*. As now constituted the section is distinguished by the distinct filaments and the small clustered petiolar glands which form a compact group at the base of the blade; as understood by Pax the section was characterized by having the calyx of the pistillate flowers "caducous."

4a. Subsect. *Urnigeræ* McVaugh, subsect. nov.

A subsectionibus ceteris generis *Cnidoscoli* filamentis libris differt.

TYPE- and only known species, *Cnidoscolus urnigerus* (Pax) Pax & Hoffm., previously included by Pax in his section *Calyptrosolen*. Material of this species has not been available for study, but the figure published by Pax (1910, p. 105) suggests a possible intermediate between *Cnidoscolus* and *Manihot*. The leaves and general aspect suggest *C. urens*, but the calyx, the

style and the androecium, if accurately interpreted and figured, preclude the possibility of merging the two species; the petiolar glands are unknown to me.

4b. Subsect. URENTES (Pax) Pax & Hoffm. Natürl. Pflanzenfam.
ed. 2. 19c: 165. 1931.

Jatropha, sect. *Jussieuia*, subsect. *Urentes* Pax, Pflanzenreich IV. 147: 96. 1910.

TYPE-SPECIES, *C. urens* (L.) Arthur. A group of about 4 species, mostly confined to lowland and coastal plain areas in warm regions. *C. urens* ranges from southern Mexico and the Lesser Antilles south to Argentina, and Mueller considered *C. herbaceus* of southeastern Mexico, and *C. stimulosus*, of southeastern United States, to be but varieties of it. *C. texanus* is a well-marked endemic of the Texas-Oklahoma region. *C. adenophilus* (Pax & Hoffm.) Pax & Hoffm., of which I have seen an isotype, is *C. urens*, and apparently *C. Loefgrenii* (Pax & Hoffm.) Pax & Hoffm. and *C. tenuifolius* (Pax & Hoffm.) Johnst., are likewise to be referred here.

C. herbaceus and *C. stimulosus* are probably best regarded as distinct from *C. urens*, but the status of the other varieties of *C. urens* proposed by Mueller [*Jatropha urens* var. *osteocarpa* (Pohl) Muell. Arg., var. *brachyloba* Muell. Arg., var. *neglecta* (Pohl) Muell. Arg., var. *Marcgravii* (Pohl) Muell. Arg.] is not so clear to me. Bondar (1942) considers all these mere forms of one species, *C. Marcgravii* Pohl, which he states is identical with *C. oligandrus* (Muell. Arg.) Pax, the *penão* of Bahia. In this last statement he is certainly in error, for Pohl's description and plate of *C. Marcgravii* show clearly that his species was a small plant very close to or identical with *C. urens*, not the large tree with 7-8 stamens which is the *penão*.

5. Sect. VITIFOLIAE (Pax) Pax & Hoffm. Natürl. Pflanzenfam.
ed. 2. 19c: 164, emend. McVaugh. 1931.

Jatropha, sect. *Vitifoliae* Pax, Pflanzenreich IV. 147: 86. 1910.

TYPE-SPECIES, *Cnidoscolus vitifolius* (Mill.) Pohl, as to plant only; not *Jatropha vitifolia* Mill. The earliest valid name for this species is apparently *C. cnicodendron* Griseb. It seems curious that Miller's name should have been applied without question by Pohl, Mueller Argoviensis, and Pax, to this species of the south-Brazilian-Argentinian region, when Miller plainly says that *Jatropha vitifolia* "was found growing naturally in Carthagera in New Spain, by the late Mr. Robert Millar," and when Miller's description indicates that he had some species of the section *Calyptrosolen*. With the exclusion of *Jatropha vitifolia* from the section here called *Vitifoliae*, there is raised the question of the propriety of retaining this sectional name which is presumably based, nomenclaturally speaking, upon *J. vitifolia*. It may be argued that the name *Vitifoliae* belongs with the species upon which it is

ostensibly based, and that the section described by Pax under this name must be renamed; it appears that this point is not covered by any rule, unless Art. 66, which mentions no rank below the subtribe, may be extended to cover it. On the other hand it may be argued that Pax had clearly in mind the circumscription of his section *Vitifoliae*, as shown by his description of the section and of the included species, so that the name *Vitifoliae* may be regarded as a descriptive name based on a composite characterization of the group, rather than directly upon *Jatropha vitifolia* Mill., which is nowhere cited as the type of the section. I have retained the name rather than provide a new one, since the choice is apparently one of taste rather than of rule.

The section includes about 14 described species, all natives of southern Brazil, Paraguay or northern Argentina except *C. peruvianua* (Muell. Arg.) Pax & Hoffm. and its supposed relatives *Jatropha basiacantha* Pax & Hoffm. and *J. diacantha* Pax & Hoffm., which are all from semi-arid cis-Andean Peru. All these species regularly have 15 or more stamens, lobed palmately veined leaves and petiolar glands like those of the *Urentes*, to which they are evidently akin.

CONCLUSION

Following is a list of all described species pertaining to *Cnidoscolus*, arranged according to sectional groups insofar as this has been possible. Names in italics are those which are definitely to be relegated to synonymy. Names published in *Jatropha*, for which there is no available combination in *Cnidoscolus*, are included but are prefixed by the initial "J"; these names are all invalid or of doubtful status in *Cnidoscolus*, and are included in these columns merely for the sake of completeness, with no intention on my part of transferring them to the latter genus.

- | | |
|--|--|
| <p>CALYPTROSOLEN</p> <p>aconitifolius</p> <p>angustidens</p> <p>calyculatus</p> <p>chayamansa</p> <p>cordifolius</p> <p>J. deutziflora</p> <p>fragrans</p> <p><i>inermiflorus</i></p> <p>†J. jaenensis</p> <p>J. Jurgenseni</p> <p>Kunthianus</p> <p>J. Liebmanni</p> <p><i>longepedunculatus</i></p> <p>longipes</p> <p><i>maculatus</i></p> <p>multilobus</p> <p><i>napaeifolius</i></p> <p>oligandrus</p> <p><i>palmatus</i></p> <p>Palmeri</p> | <p>J. <i>Papaya</i></p> <p>paucistamineus</p> <p>polyanthus</p> <p>Pringlei</p> <p>pubescens (Pax) P. & H.</p> <p>†J. pyrophora</p> <p>J. <i>quinqueloba</i> Sessé</p> <p>quinquelobatus</p> <p>rotundifolius</p> <p>Shrevei</p> <p>tepiqueensis</p> <p>tubulosus</p> <p>†J. vitifolia Mill.</p>
<p>VITIFOLIAE</p> <p>albomaculatus</p> <p>appendiculatus</p> <p>bahianus</p> <p>J. basiacantha</p> <p>campanulatus</p> <p>cnicodendron</p> |
|--|--|

<i>J. diacantha</i>	CNIDOSCOLUS
<i>hasslerianus</i>	(Victorinia)
<i>horridus</i>	<i>acerandrus</i>
<i>peruvianus</i>	<i>J. regina</i>
<i>J. Sellowiana</i>	(Phyllacanthae)
<i>tetracyclus</i>	<i>bellator</i>
<i>Ulei</i>	<i>lobatus</i>
<i>vitifolius</i> Pohl	<i>phyllacanthus</i>
	<i>quercifolius</i>
	<i>repandus</i>
<i>JUSSIEULA</i>	(Eucnidoscolus)
(<i>Urnigeræ</i>)	<i>hamosus</i>
<i>urnigerus</i>	<i>hypoleucus</i>
(<i>Urentes</i>)	<i>leuconeurus</i>
<i>adenophilus</i>	<i>loasoides</i>
<i>herbaceus</i>	<i>maracayensis</i>
<i>infestus</i>	<i>obtusifolius</i>
† <i>Loefgrenii</i>	<i>pubescens</i> Pohl
<i>Maregravii</i>	<i>serrulatus</i>
<i>Michauxii</i>	<i>subinteger</i>
<i>neglectus</i>	
<i>osteocarpus</i>	
<i>quinguelobus</i> Pohl	PLATYANDRAE
<i>stimulosus</i>	<i>Matosii</i>
† <i>tenuifolius</i>	<i>platyandrus</i>
<i>texanus</i>	Rangel

DOUBTFUL SPECIES

The following species cannot be assigned to any section: 1. *Jatropha aculeatissima* Colla, Herb. Pedem. 5: 112. 1836, based on a Brazilian plant collected by Pedro d'Agoa. 2. *Jatropha octandra* Sessé in Cerv. Supl. Gaz. Lit. 4. 1794, based on a Mexican collection. 3. *Cnidoscolus Souzae* McV. See above.

EXCLUDED SPECIES

Cnidoscolus surinamensis Miq. Linnaea 18: 749 (1844) is a synonym of *Croton lobatus*.

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JUNIPERUS VIRGINIANA, J. HORIZONTALIS AND J. SCOPULORUM—II. HYBRID SWARMS OF J. VIRGINIANA AND J. SCOPULORUM

NORMAN C. FASSETT ♂

J. virginiana and *J. scopulorum* differ in ten sets of characters;¹ the five most conveniently used are listed in tables 1 and 2. In table 1, each horizontal line represents one tree in a colony of *J. virginiana*. The epidermal cells of the leaves vary from 5 to 20 μ in width;² each figure in the first column was obtained by measuring 30 cells and averaging. The averages range from 9.7–12.2 μ ; in a colony of *J. scopulorum* (table 2) they range from 14.8–12.5 μ . Column 2 in table 1 shows every individual of *J. virginiana* to have overlapping leaves, while in *J. scopulorum* (table 2) the leaves rarely overlap, and then but very little. In column 3, the foliar gland of *J. virginiana* is in every case seen to be shorter than the distance from the gland to the tip of the leaf, while in *J. scopulorum* (table 2, third column) the gland always exceeds this distance. The leaf tips are always acute in *J. virginiana* (table 1, fourth column) and always blunt in *J. scopulorum* (table 2, fourth column). Column 4 is incomplete in the tables, because not all the trees bear carpellate cones. In *J. virginiana* 0–33 per cent of the cones are on hooked peduncles, and the majority of them are on straight peduncles. In *J. scopulorum* 8–70 per cent of the peduncles are hooked. Therefore, a figure between 8 and 33 may be either species.

TABLE 1. Ten individuals of *J. virginiana* from Portland, Connecticut.

Average width of epidermal cells, in micra	Leaves overlapping or not overlapping	Gland shorter than distance to tip or leaf, or longer	Leaf tips	Per cent of peduncles curved
9.7	Overlapping	Shorter	Acute	...
10.0	Overlapping	Shorter	Acute	0
10.3	Overlapping	Shorter	Acute	...
11.0	Overlapping	Shorter	Acute	8
11.3	Overlapping	Shorter	Acute	0
11.3	Overlapping	Shorter	Acute	...
11.7	Overlapping	Shorter	Acute	...
11.8	Overlapping	Shorter	Acute
11.8	Overlapping	Shorter	Acute
12.2	Overlapping	Shorter	Acute

¹ Fassett, Bull. Torrey Club 71: 410–418. 1944.

² For table showing the proportions of each width class on individual trees, see Fassett, *l. c.*

TABLE 2. *Ten individuals of J. scopulorum from Upper Tunnel, Bad Lands of South Dakota.*

Average width of epidermal cells, in micra	Leaves overlapping, or not overlapping	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
13.3	Not	Longer	Obtuse	..
13.5	Not	Longer	Obtuse	39
14.5	Not	Longer	Obtuse	62
15.0	Not	Longer	Obtuse	47
15.2	Not	Longer	Obtuse
16.2	Slightly	Longer	Obtuse
16.3	Slightly	Longer	Obtuse	..
16.6	Slightly	Longer	Obtuse	17
16.8	Slightly	Longer	Obtuse	36
17.5	Not	Longer	Obtuse	50

That the single table here presented for each species is practically identical with similar tables which have been made for each species has already been demonstrated in the first paper of this series;³ the proviso was there made, however, that these characters do not remain constant in areas where two species of the group grow together. Such areas exist in the Dakotas and Nebraska, where the ranges of *J. virginiana* and *J. scopulorum* overlap.

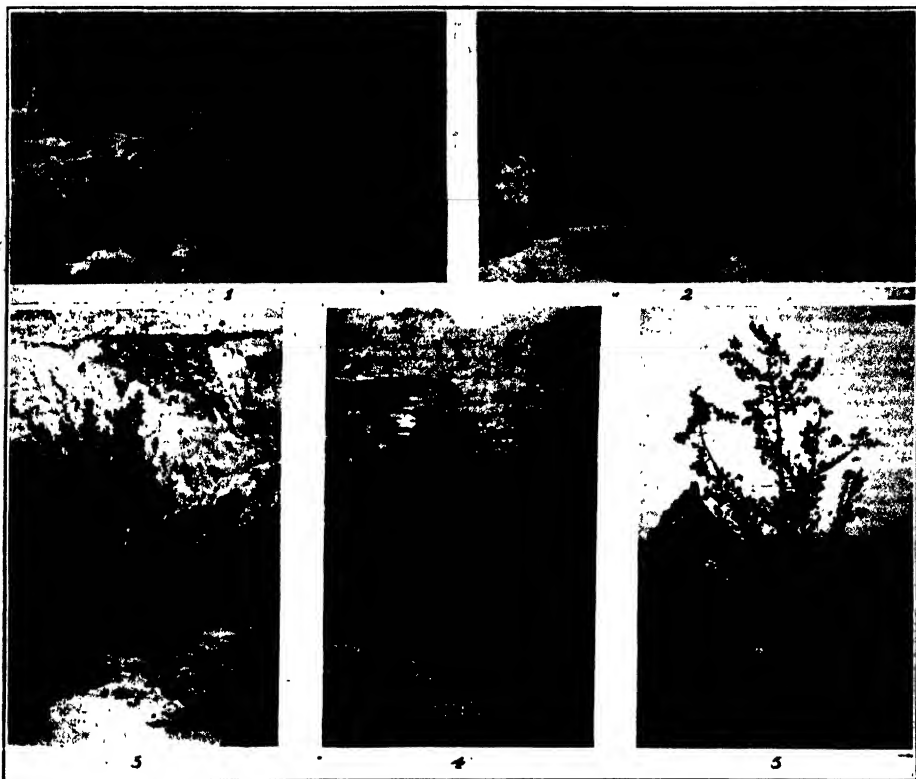
In the Arnold Arboretum there is a sheet of characteristic *J. virginiana* from Dell Rapids, near the eastern border of South Dakota, and several sheets of equally characteristic *J. scopulorum* from the Black Hills, at its western border. The writer has made mass collections at Wasta and at Upper Tunnel (in the northwestern part of the Bad Lands), and both collections consist entirely of pure *J. scopulorum*. But at the localities shown by figures on the map are colonies of red cedars showing various recombinations of the characters of the two species.

TABLE 3. *Nine individuals of a hybrid swarm of J. virginiana and J. scopulorum from Chamberlain, South Dakota.*

Average width of epidermal cells, in micra	Leaves overlapping or not overlapping	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
11.0	Overlapping	Shorter	Acute	41
11.3	Overlapping	Shorter	Acute	41
*11.3	Overlapping	Shorter	Acute	11
*11.3	Overlapping	Shorter	Acute	29
11.8	Overlapping	Shorter	Acute	38
13.0	Not	Shorter	Acute
13.5	Overlapping	Shorter	Acute
14.3	Overlapping	Shorter	Acute	..
16.5	Not	Shorter	Acute	45

³ Fassett, l. c.

At Chamberlain, S. D. (6 in figure 6), twigs from nine trees were examined (table 3). These all agree with *J. virginiana* in having short foliar glands and acute leaf tips, and in all but two the leaves overlap. But the trees which bear cones all have proportions of hooked peduncles which agree with *J. scopulorum* much better than with *J. virginiana*. The epidermal cells, moreover, are characteristic of *J. scopulorum* in four cases. Were one to encounter each of these as a separate herbarium sheet, only two individuals (indicated by asterisks in table 3) would be identified as *J. virginiana*; the



FIGS. 1-5. *Juniperus* at Cedar Pass, Bad Lands of South Dakota.

first two would be called *J. virginiana* but the large percentages of hooked peduncles, and the other five could be characterized only as having mixtures of characters of each. These trees grow in low ground along the Missouri River, just west of Chamberlain, in a fairly moist habitat that suggests *J. virginiana* rather than *J. scopulorum*; furthermore, the trees look like the eastern species. The colony might be described as consisting of *J. virginiana* with a slight admixture of *J. scopulorum*, expressed by the high percentages of hooked peduncles and the wide epidermal cells of many trees.

The traveller from the east usually enters the Bad Lands of South Dakota at Cedar Pass (4 in figure 6), obviously named for the cedar-filled canyon whose rim is skirted by the highway. Of the 40 individuals collected (table 4) none can be identified as pure *J. virginiana*, and but one (marked with an

TABLE 4. Forty individuals of a hybrid swarm of *J. virginiana* and *J. scopulorum* from Cedar Pass, Bad Lands of South Dakota.

Average width of epidermal cells, in micra	Leaves overlapping or not overlapping	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
11.3	Not	Shorter	Obtuse
12.3	Overlapping	Shorter	Obtuse	45
12.5	Overlapping	Shorter	Acute	50
12.5	Overlapping	Shorter	Obtuse
12.7	Overlapping	Shorter	Obtuse
12.7	Not	Longer	Obtuse	70
12.8	Not	Longer	Obtuse
12.8	Overlapping	Shorter	Obtuse
13.0	Overlapping	Shorter	Obtuse	..
13.2	Overlapping	Shorter	Obtuse	..
13.2	Overlapping	Shorter	Obtuse
13.3	Not	Longer	Obtuse
13.3	Overlapping	Longer	Obtuse	..
13.5	Overlapping	Shorter	Acute
13.5	Overlapping	Shorter	Obtuse
13.7	Overlapping	Shorter	Acute	..
13.8	Overlapping	Shorter	Obtuse	..
14.0	Overlapping	Shorter	Acute	..
14.2	Overlapping	Shorter	Acute
14.2	Overlapping	Shorter	Obtuse
*14.2	Not	Longer	Obtuse	..
14.3	Overlapping	Shorter	Obtuse
14.3	Overlapping	Shorter	Obtuse
14.5	Overlapping	Shorter	Obtuse	50
14.8	Overlapping	Shorter	Obtuse	..
14.8	Overlapping	Shorter	Acute	6
14.8	Overlapping	Shorter	Acute
15.0	Overlapping	Shorter	Obtuse
15.0	Not	Shorter	Acute	..
15.2	Overlapping	Shorter	Acute
15.3	Overlapping	Shorter	Acute
15.5	Overlapping	Shorter	Acute	..
16.3	Overlapping	Shorter	Obtuse	..
16.3	Overlapping	Shorter	Acute	..
16.3	Not	Shorter	Acute	..
16.5	Overlapping	Shorter	Obtuse
16.6	Overlapping	Shorter	Obtuse
17.7	Not	Shorter	Acute	..

asterisk) is pure *J. scopulorum*. Throughout the colony, the characters of the two species seem to be thoroughly scrambled, occurring in all possible combinations. Some of the trees look like *J. virginiana*, some look like *J. scopulorum*, and many have a peculiar appearance scarcely characteristic of either species (figs. 1-5). The combination of characters most frequently found is

TABLE 5. Six individuals of a hybrid swarm of *J. virginiana* and *J. scopulorum* from a bluff south of White River, 8 miles south of Interior, South Dakota.

Average width of epidermal cells, in micra	Leaves overlapping or not overlapping	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
11.7	Overlapping	Longer	Obtuse	..
13.3	Overlapping	Longer	Obtuse	61
*15.6	Not	Longer	Obtuse	..
*15.8	Not	Longer	Obtuse	..
16.0	Overlapping	Longer	Obtuse	47
16.5	Not	Longer	Obtuse	17

J. virginiana in all but the wide epidermal cells of the leaves; of the 11 individuals showing this combination but one bears cones, and this one has 6 per cent of the peduncles hooked, as is also characteristic of *J. virginiana*.

A few miles south of Cedar Pass (5 in figure 6; table 5), to the south of the White River, six cedars were collected on a hot dry hillside. That these trees had pointed crowns, instead of the rounded ones usually characteristic of *J. scopulorum*, is probably not significant, for that species sometimes has pointed crowns. Three of the trees are characteristic *J. scopulorum*, and are indicated by asterisks in table 5, while each of the other three shows one or more characters of *J. virginiana*. In contrast to the colony at Chamberlain, at the eastern limit of observed influence of *J. scopulorum*, this may be described as a colony of *J. scopulorum* with some admixture of *J. virginiana* representing the farthest western influence of the latter species.

TABLE 6. Sixteen individuals of a hybrid swarm of *J. virginiana* and *J. scopulorum* from Ainsworth, Nebraska.

Average width of epidermal cells, in micra	Leaves overlapping or not overlapping	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
10.8	Not	Shorter	Acute	..
*11.0	Overlapping	Shorter	Acute	0
11.0	Not	Shorter	Acute
*11.5	Overlapping	Shorter	Acute	..
12.2	Not	Shorter	Acute	0
12.2	Not	Shorter	Acute
12.3	Overlapping	Shorter	Acute
13.0	Overlapping	Shorter	Acute
13.2	Overlapping	Shorter	Obtuse
13.3	Overlapping	Shorter	Acute
13.5	Overlapping	Shorter	Acute	0
13.5	Overlapping	Shorter	Acute	0
13.5	Not	Shorter	Acute
13.6	Overlapping	Shorter	Acute
14.6	Not	Shorter	Acute
15.0	Not	Shorter	Acute

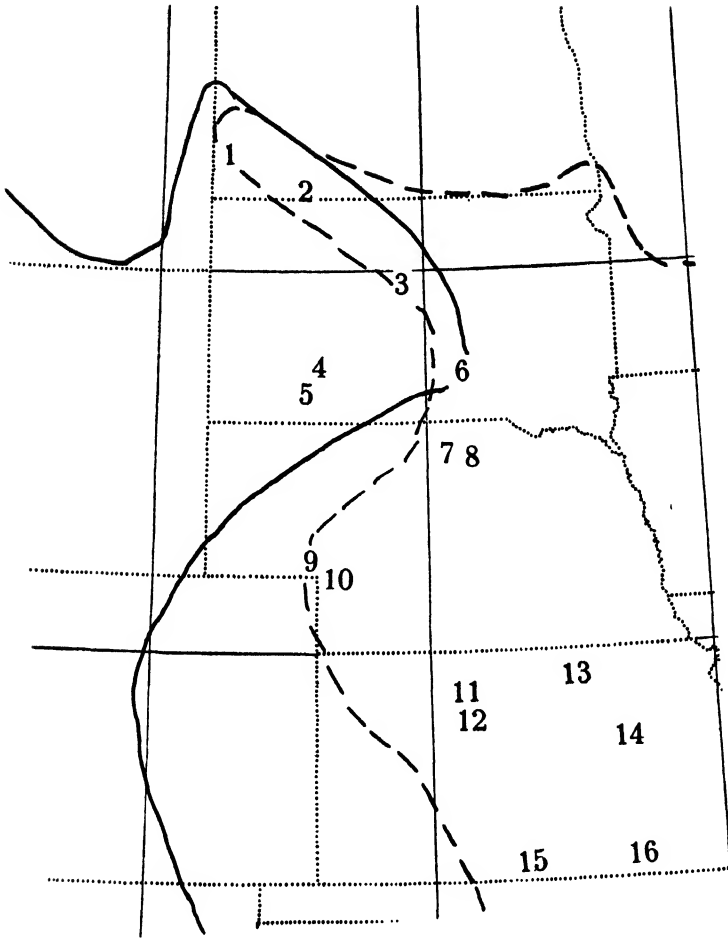


FIG. 6. Heavy line: approximate northeastern limits of *J. scopulorum*. Broken line: approximate northwestern limits of *J. virginiana*. 1-16: locations of herbarium specimens or mass collections showing some mixture of characters of the two species. 1. Medora, Billings Co., N. D. 2. Paradise, Grant Co., N. D. These two specimens in Herb. N. D. Agr. Coll. 3. Mouth of Big Cheyenne River, S. D., collected by Lewis & Clark in 1804. 4. Mass collection from Cedar Pass, S. D., described in table 4. 5. Mass collection from Interior, S. D., described in table 5. 6. Mass collection from Chamberlain, S. D., described in table 3. 7. Mass collection from Johnstown, Neb., very similar to the next. 8. Mass collection from Ainsworth, Neb., described in table 6. 9. Mass collection from Lewellen, Neb., described in table 7. 10. Mass collection from Ogalalla, Neb., described in table 8. 11. Specimen from Rockport, Kans., with epidermal cells averaging $17.6\ \mu$ in width. This and all the following specimens are in Herb. Kans. State Coll. 12. Specimens from Ellis Co., Kans., with epidermal cells averaging $16.2\ \mu$ in width. 13. Specimen from Cloud Co., Kans., with epidermal cells averaging $15.0\ \mu$ in width. 14. Specimen from Morris Co., Kans., with epidermal cells averaging $14.3\ \mu$ in width. 15. Specimens from Medicine Lodge, Barber Co., Kans., with epidermal cells averaging $14.3\ \mu$ in width. 16. Specimen from Chautauqua Co., Kans., with epidermal cells averaging $14.3\ \mu$ in width.

TABLE 7. *Twelve individuals of a hybrid swarm of J. virginiana and J. scopulorum from Lewellen, Nebraska.*

Average width of epidermal cells, in micra	Leaves overlapping or not overlapping	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
12.0	Overlapping	Shorter	Acute	19
12.3	Overlapping	Shorter	Acute	...
12.5	Overlapping	Shorter	Obtuse	0
12.5	Overlapping	Shorter	Obtuse	5
13.0	Overlapping	Shorter	Acute	.
13.2	Overlapping	Shorter	Acute	0
13.8	Overlapping	Shorter	Acute	7
14.0	Overlapping	Shorter	Acute	25
14.0	Overlapping	Shorter	Acute	.
14.5	Overlapping	Shorter	Acute	12
14.5	Overlapping	Shorter	Acute	20
14.5	Overlapping	Shorter	Acute	5

A fragmentary specimen at the Arnold Arboretum, collected by Lewis & Clark on October 28, 1804, at "Little or Lookout Point of the Missouri at or near the mouth of the Big Cheyenne River" (3 in figure 6) has the blunt leaves with wide epidermal cells of *J. scopulorum*, and the overlapping leaves with gland length less than the distance to the tip as in *J. virginiana*; it probably represents one individual from a hybrid swarm.

About 90 miles south of Chamberlain, two mass collections were made, at Johnstown and Ainsworth, Nebraska (7 & 8, respectively, in figure 6). They are so similar that only the collection at Ainsworth is presented in detail (table 6). These trees grow along the banks of, and at some distance

TABLE 8. *Twelve individuals of a hybrid swarm of J. virginiana and J. scopulorum from Ogallala, Nebraska.*

Average width of epidermal cells, in micra	Leaves overlapping or not overlapping	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
12.7	Overlapping	Shorter	Acute	.
13.2	Overlapping	Shorter	Obtuse	19
13.2	Overlapping	Shorter	Acute	.
13.3	Overlapping	Shorter	Acute	5
13.6	Overlapping	Shorter	Acute	.
14.3	Overlapping	Shorter	Acute	20
14.3	Overlapping	Shorter	Acute
15.3	Overlapping	Shorter	Acute
16.0	Overlapping	Shorter	Acute
16.5	Overlapping	Shorter	Acute	.
17.8	Overlapping	Shorter	Acute	50
18.7	Overlapping	Shorter	Acute	25

back from, a small stream.⁴ They all look like *J. virginiana*, and as in the colony at Chamberlain there is some admixture of *J. scopulorum* so that but two individuals (marked by asterisks) would be unquestionably identified as *J. virginiana*. However, here a different set of characters from *J. scopulorum* is infused into *J. virginiana*. There are no hooked peduncles on any of the four fruiting plants, but nearly half the trees have the non-overlapping leaves of *J. scopulorum*. One tree has the blunt leaves of *J. scopulorum*, but none has the long glands characteristic of the western species. As at Chamberlain, the averages of leaf size run the gamut from *J. virginiana* to *J. scopulorum*, with many intermediates.

TABLE 9. Summary of tables 1-8; tendencies of characters in each region.

	Epidermal cells	Overlapping of leaves	Length of foliar gland	Leaf tips	Peduncles
Portland, Conn.	All <i>virginiana</i>	All <i>virginiana</i>	All <i>virginiana</i>	All <i>virginiana</i>	All <i>virginiana</i>
Scattered in Kans.	Approach <i>scopulorum</i>	All <i>virg.</i>	All <i>virg.</i>	All <i>virg.</i>	All <i>virg.</i>
Ogallala, Neb.	Range from <i>virg.-scop.</i>	All <i>virg.</i>	All <i>virg.</i>	11 out of 12 <i>virg.</i>	4 out of 5 <i>virg.</i>
Lewellen, Neb.	Range from <i>virg.-scop.</i>	All <i>virg.</i>	All <i>virg.</i>	9 out of 12 <i>virg.</i>	All <i>virg.</i>
Ainsworth, Neb.	Range from <i>virg.-scop.</i>	7 out of 16 <i>virg.</i>	All <i>virg.</i>	All <i>virg.</i>	All <i>virg.</i>
Chamberlain, S. D.	Range from <i>virg.-scop.</i>	7 out of 9 <i>virg.</i>	All <i>virg.</i>	All <i>virg.</i>	All <i>scop.</i>
Cedar Pass, S. D.	Range from <i>virg.-scop.</i>	30 <i>virg.</i> 8 <i>scop.</i>	33 <i>virg.</i> 5 <i>scop.</i>	14 <i>virg.</i> 24 <i>scop.</i>	1 <i>virg.</i> 4 <i>scop.</i>
Interior, S. D.	Range from <i>virg.-scop.</i>	3 <i>virg.</i> 3 <i>scop.</i>	All <i>scop.</i>	All <i>scop.</i>	All <i>scop.</i>
Upper Tunnel, S. D.	All <i>scop.</i>	All <i>scop.</i>	All <i>scop.</i>	All <i>scop.</i>	All <i>scop.</i>

Two large mass collections have been made in southwestern Nebraska (9, 10 in figure 6) by Dr. Walter Kiener; from each of these 12 individuals have been examined and the results presented in tables 7 and 8. Like the two mass collections in northern Nebraska, they are very similar, indicating some degree of regional uniformity.⁵ For the most part they are all fairly pure *J. virginiana*, but the influence of *J. scopulorum* is shown by the tendency toward wide epidermal cells.

The material from Kansas, loaned to me from Kansas State College by Prof. F. C. Gates, is mostly pure *J. virginiana*, but a few sheets from scattered regions (11-16 in figure 6) show the wide epidermal cells of *J. scopulorum*. Three mass collections from Kansas were examined, and all proved

⁴ Dr. Walter Kiener writes me that this stream is Bone Creek.

⁵ Meaning that the colonies within a region vary in the same way, not that all individuals in a region are alike.

to be pure *J. virginiana*: Dr. Gates made a very large collection in Riley County, of which 142 individuals were studied; Rev. S. V. Fraser collected 9 individuals in Cloud County; and at Sedan, Chautauqua County, 12 individuals were collected by Homer Stephens, L. H. Shinnors and Grant Cottam.

CONCLUSIONS

Colonies in the east are pure *J. virginiana*; in Kansas occasional plants show a slight tendency toward *J. scopulorum*; in Nebraska this tendency is stronger; in the Bad Lands of South Dakota colonies show a completely scrambled mixture of characters of the two, then grade off to pure *J. scopulorum* in the west. These facts are shown in tabular form in table 9.

The mixture at Cedar Pass, where there seems to be no correlation of characters, is probably the result of a comparatively recent meeting of the two present species. There has probably not been time for a scattering of the variability,⁶ and there have probably been successive migrations of one or both parents, which have kept variability at a high level. At Chamberlain (table 3; 6 in figure 6) the meeting was probably farther in the past, and back-crosses with *J. virginiana* have been possible, so that the *J. scopulorum* characters have been largely swamped out, persisting strongly in the hooked peduncles and to some extent in the tendency of some individuals to have wide epidermal cells. The situation is much the same at Ainsworth (table 6; 8 in figure 6), but, as might be expected, scattering of the variations has left a set of *J. scopulorum* characters, different from the set left at Chamberlain. In Kansas, where there is a gap between the present ranges of the two species, the tendency of occasional individuals of *J. virginiana* toward having the wide epidermal cells of *J. scopulorum* suggests an ancient incursion of the range of the latter species into that of the former.

The writer wishes to express appreciation to the Wisconsin Alumni Research Foundation for grants making possible the studies of these trees over a large part of their ranges, to the Arnold Arboretum for loans of material, and to the several gentlemen mentioned in the text, who have made mass collections in critical areas.

SUMMARY

Where *Juniperus virginiana* grows by itself, and where *J. scopulorum* grows by itself, each species retains pure specific characteristics, except in areas in the western part of the range of *J. virginiana* where certain tendencies toward *J. scopulorum* suggest an ancient incursion of that species. Where the ranges of the two species meet, all recombinations of the characters of each occur in individuals of one colony.

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⁶ See Dobzhansky, *Genetics and the origin of species*, p. 130, 132.

SUPPLEMENTARY NOTES ON AMERICAN LABIATAE—III¹

CARL EPLING

STACHYS

S. LAMIOIDES Benth. COLOMBIA: COMISARÍA DEL PUTUMAYO: alta cuenca del río Putumayo en El Valle de Sibundoy extremo E., junto a San Francisco, 2200 m., *Cuatrecasas* 11548.

S. calcicola Epling, sp. nov. Herba perennis prostrata repens et in nodis radicibus crassiusculis radicanibus, caulibus pilis gracilibus patentim villosis, internodiis ramulorum floriferum quam folia brevioribus vel paulo longioribus, ramulorum procurentium duplo triplove longioribus; foliorum laminis ovalibus, 1.5-2.5 cm. longis, crenato-serratis, subtus venulosis, paginis ambabus pilis gracilibus mollibus appress-hirsutis; petiolis plerumque 5-10 mm. longis; floribus tribus in foliorum deminutorum supremorum dispositis, glomerulis plus minusve confertis; calycem florentium tubo 3-4 mm. longo, extus molliter appresso-hirsuto, dentibus deltoideis 1.5-2 mm. longis, obtusis, muticis; corollarum tubo 6-7 mm. longo, sat crasso, integro, intus supra tubi basim 3 mm. transverse annulato, labia superiore 6-7 mm. alta; staminibus e tubo sub galeam 3 mm. exsertis. GUATEMALA: DEPT. HUEHUETENANGO: vicinity of Chémal, summit of Sierra de los Cuchumatanes, alt. 3700-3750 m., rocky lime outcrops with *Juniperus Standleyi*, August 8, 1943, *Steyermark* 50266, TYPE (UCLA). In pubescence, as well as habit, this species suggests *S. ajugoides* of California or *S. sericea* of Chile, but the annulus in the corolla tube of these species is oblique, rather than transverse. Perhaps it is more nearly allied to the former.

S. glechomoides Epling, sp. nov. Herba perennis decumbens caulibus gracilibus debilibus utrimque solim ad angulos pilis brevibus gracilibus retrorso-appressis sat dense vestitis internodiis quam folia duplo longioribus; foliorum laminis cordato-ovatis, etiam rotundatis, 1.5-2.5 cm. longis, in apice obtusis vel infimis rotundatis, paginis ambabus pilis gracilibus sparse vestitis vel inferiore glabra, marginibus obtuse crenatis, crenis plerumque 15-20; petiolis gracilibus 20-30 mm. longis, hirsutis; floribus plerumque tribus in foliorum supremorum et bracteorum deminutorum axillis dispositis, glomerulis inter se 1-3 cm. distantibus; calycem florentium tubo 3-3.5 mm. longo, extus sparse hirtellis, dentibus 1.5-2.5 mm. longis, acuminatis, ciliolatis, spinulosis, in maturitate non visis; corollarum rosearum tubo sat crasso, integro, 9-10 mm. longo, intus circiter 3 mm. supra basim transverse annulato, labia superiore 4-5 mm. alta; staminibus 2.5-3 mm. e tubo sub galeam exsertis. GUATEMALA: DEPT. HUEHUETENANGO: Wet cloud forest at Cruz de Simón, between San Mateo Ixtatan and Nucá, Sierra de los Cuchumatanes, alt. 2600-3000 m., July 31, 1942, *Steyermark* 49789, TYPE (UCLA). Wet cool cloud forest between Cananá and Quetzal, Cerro Cananá, between Micapuxlac and Cananá, Sierra de los Cuchumatanes, alt. 2500-2800 m., July 18, 1942, *Steyermark* 49102. It is not without reluctance that

¹ See Bull. Torrey Club 67: 509-534. 1940; 68: 552-568. 1941.

I describe this species in so difficult a genus and section. The species is allied to *S. costaricensis* and much resembles the type of that species in habit. The distinctive appressed pubescence which occurs only along the angles of the stem and the leaf margins suggests that it is not the same. The crenations of the leaf margins of *S. costaricensis* are usually 30–40 in number and are generally more acute; the pubescence is of a different sort, not confined to the angles, and is retrorse but not appressed.

S. LINDENII Benth. GUATEMALA: DEPT. SUCHITEPEQUEZ: Volcan Santa Clara between Finca El Naranjo and upper slopes, 1250–6250 m., *Steyermark* 46694. Chiapas. Mt. Tacana, 2400–4038 m., *Matuda* 2310. What may prove to be an outlying variant of this species has been collected by *Gentry* (No. 1144) in Mexico at San Bernardo, Sonora. It is a more slender, less hispid plant, with more slender corollas and shorter calyx teeth.

S. ERIANTHA Benth. GUATEMALA: DEPT. HUEHUETENANGO: between Tojquia and Caxín bluff, summit of Sierra de los Cuchumantanes, 3700 m., *Steyermark* 50219. This is the first collection I have seen from Central America of this species, which hitherto has been known only from Mexico and northern South America. This collection resembles the South American, rather than the Mexican specimens.

S. COSTARICENSIS Briq. GUATEMALA: DEPT. ZACAPA: upper slopes, along Río Repollal to summit of mountain, 2100–2400 m., *Steyermark* 42534. *Steyermark* 42940. Dept. Zacapa, between Santa Rosalía de Marmol and Vegas, may represent the same species, but the calyces are large and atypical. *Steyermark* 48944, collected near Nucapuxlac, may be a depauperate form.

S. RADICANS Epling. GUATEMALA: DEPT. HUEHUETENANGO: alpine areas in vicinity of Tunimá, Sierra de los Cuchumatanes, 3400–3500 m., *Steyermark* 48394. Also collected in the same region by *Skutch* (No. 1216, 1225), but not previously known from Central America.

S. GUATEMALENSIS Epling. GUATEMALA: DEPT. HUEHUETENANGO: between Barillas and Cerro Victoria, Sierra de los Cuchumatanes, 1700–1800 m., *Steyermark* 49694. Very similar to the type which was collected in Alta Vera Paz.

S. (?) NUBILORUM Epling. GUATEMALA: DEPT. HUEHUETENANGO: vicinity of Chemal, summit of Sierra de los Cuchumatanes, 3700–3750 m., *Steyermark* 50315. The type of this species was collected in Chimaltenango at Santa Elena. The present specimen differs in regard to leaf shape, pubescence and calyx, but not improbably represents the same species.

S. COCCINEA Jacq. GUATEMALA: HUEHUETENANGO: Cerro Pixpíx, above San Ildefonso Ixtahuacán, *Steyermark* 50576. Add the following synonyms: *Cedronella pallida* Lindl. Bot. Reg. pl. 29. 1846. *Brittonnastrum pallidum* Briq. in E. & P. Nat. Pfl. 4(3A): 235. 1897.

S. LANATA Jacq. PERU: HUANCANELICA: Prov. Castrovirreina, near Cordova, 3050–3300 m., among rock fences, *Metcalf* 30264. A Mediterranean cultigen, perhaps naturalized here.

S. PERUVIANA Domb. ex Benth. PERU: AYACUCHO: Prov. Lucanas, 6 km. from Puquio, 3200 m., *Metcalf* 30334. Very similar to Dombey's type. Although scarcely annulate, the corolla tube is hirtellous within.

MINTHOSTACHYS

The putative species of *Minthostachys* range widely and are differentiated on slender grounds of pubescence, calyx differences, corolla size and leaf habit. One is frequently led to doubt the existence of more than one highly variable species. Nevertheless, similar or nearly identical forms are frequently found in various parts of the range. The following are of interest.

M. SPICATA (Benth.) Epl! PERU: HUANCANELICA: Prov. Castrovirreina, near Cordova, 3050-3300 m., *Metcalf* 30285. AYACUCHO: Prov. Lucanas, along road Puquio to Lucanas, 3200 m., *Metcalf* 30329.

M. MOLLIS (Kunth) Griseb.! PERU: LIMA: Prov. Huarochiri, valley of Rio Rimac, near Lima-Oroyo highway, 90 km. east of Lima, 2900 m., *Good-speed and Weberbauer* 33055. Very similar to Kunth's type found in Ecuador, probably near Cuenca, and to *Lehmann* 5823 from the same locality.

M. TOMENTOSA (Benth.) Epl.! PERU: CUZCO: Prov. Quispicanchis, near Marcapata, 300 m., *Metcalf* 30732. Very like Bentham's type collected by Ruiz and Pavon, possibly in Junin, and like Killip and Smith 24252, also collected in Junin. *Weberbauer* 7879, collected at Marcapata, is therefore more probably *M. tomentosa* rather than *M. setosa*, as previously determined by me. *Metcalf* 30724, also from Marcapata, is probably also referable here, but differs not only in aspect but especially in the distinctly ovate-acuminate calyx teeth.

M. SETOSA (Briq.) Epl.? PERU: Prov. Sandia, near Limbani, 3200-3450 m., *Metcalf* 30499. Very similar in floral structure and pubescence to Briquet's type, collected by Kuntze in Bolivia at Rio Juntas, but the leaves larger and less acuminate. Plants with the same flowers also occur in Ecuador (BOLIVAR: *Penland* 674) and in Peru (*Killip and Smith* 22308). They differ in aspect and pubescence.

LEPECHINIA

L. CAULESCENS (Ort.) Epling. MEXICO: SINALOA: Ocurahui, Sierra Surotato. Pine forest, 6000-7000 ft., *Gentry* 6171. GUATEMALA: DEPT. HUEHUETENANGO: near Soloma, Sierra los Cuchumatanes, 2400 m., *Steyermark* 49966.

L. HUMILIS Epling. COLOMBIA: DEPT. DEL BOYACÁ: Paramo de Guina, 3200 m., *Barriga* 9794.

L. SALVIAEFOLIA (Kunth) Epling. COLOMBIA: DEPT. DE BOYACÁ: Paramo de Santa Rosa, entre Santa Rosa de Viterbo y Cerinza, 2950 m., *Cuatrecasas and Barriga* 9725.

L. BULLATA (Kunth) Epling. COLOMBIA: COMISARÍA DEL PUTUMAYO: alta cuenca del río Putumayo en El Valle de Sibundoy extremo E., junto a San Francisco, 2200 m., *Cuatrecasas* 11545.

L. VESICULOSA (Benth.) Epling. *Soukup 441*, labelled as coming from Puno, Peru, was in fact collected at Macchupichu, Cuzco (fide E. P. Killip).

L. RADULA (Benth.) Epling. PERU: DEPT. HUANCANELICA: Prov. Taya-caya, Surcubamba, 2600 m., *Stork and Horton 10355*.

Lepechinia (Speciosae) *sagittata* Epling. sp. nov. Herba perennnis in specimine suppetente vivo altitudine circiter 40 cm. caulibus paucis ascendentibus pilis pustulato-ramosis et glandulosis subsessilibus conspersis, internodiis quam folia brevioribus; foliorum laminis pulchre sagittatis, viridibus, mediis 5-6 cm. longis, 3-3.5 latis, acutis, marginibus crenato-serratis, pagina superiore rugosa, ambabus pilis ramosis et glandulis sessilibus conspersis, petiolis 2-2.5 cm. longis; floribus tribus in verticillastris, bracteis perstatis membranaceis subtentis, in spicis interruptis dispositis, glomerulis inter se 1-1.5 cm. distantibus; calycem florentium tubo 3.5 mm. longo, obliquo, extus sparse hispidulo et glandulis sessilibus consperso, dentibus acuminatis, superioribus circiter 1 mm. longis, inferioribus duplo longioribus, in maturitate tubo campanulato, 8 mm. longo, dentibus superioribus 2 mm., inferioribus 3 mm. longis; corollarum albidarum tubo 6 mm. longo, supra basim 2.5 mm. piloso-annulato; nuculis atris, circiter 2 mm. longis.

Grown at Los Angeles from seeds collected by Dr. T. H. Goodspeed in western Argentina, TYPE at the University of California (Los Angeles).

L. MEYENI (Walp.) Epl. PERU: HUANCANELICA: Prov. Castrovirreina, near Cordova, 3050-3300 m., *Metcalfe 30265*.

SCUTELLARIA

27. *S. TESSELLATA* Epling. A collection made by Waterfall (No. 5087) in Culberson County, Texas, may represent a quite glabrous form of this species. If so, it is the first of the section in which pubescence is wanting. No nutlets are preserved, hence determination is inconclusive. The leaves, however, suggest that an undescribed entity is represented, for they are widest near the base, are obscurely and rather coarsely dentate, somewhat after the habit of *S. cardiophylla*, and are differently veined, the principal veins tending to arise near the base.

62. *S. (?) PSEUDOCAERULEA* Briq. MEXICO: SINALOA: Ocurahui, Sierra Surotato. Pine forest, 6000-7000 ft. *Gentry 6313*. Allied to this species of central Mexico and assuredly one of the *S. caerulea* species group. The only other species of this section known from Sinaloa is *S. russelioides* of quite different habit.

75. *S. ORICHALCEA* J. D. Smith. GUATEMALA: DEPT. IZABAL: along Rio Frio and tributaries, 75-150 m., *Steyermark 41573*.

95. *S. MOCINIANA* Benth. GUATEMALA: DEPT. HUEHUETENANGO: Cerro Chiblac, between Finca San Rafael and Ixcán, Sierra de los Cuchumatanes, 1200-2000 m., *Steyermark 49155*. Apparently this species, heretofore known only from the state of Vera Cruz, Mexico.

98. *S. (?) COCCINEA* Kunth. COMISARÍA DEL PUTUMAYO: selva higrofila entre Quebrada de la Hormiga y San Antonio del Güarmes, 330 m., *Cuatrecasas 11160*.

110. *S. SELERIANA* Loesen. GUATEMALA: DEPT. ZACAPA: upper slopes, along Rio Repollal to summit of mountain, 2100-2400 m., *Steyermark 42472*. The nutlets of this specimen are black and minutely papillate.

112. *S. PERILOMIA* Epling. ECUADOR: BOLIVAR: Magdalena to Balsapampa, *Haught* 3288.

MONARDA

M. AUSTROMONTANA Epling. MEXICO: SINALOA: Ocurahui, Sierra Surotato. Scattered colonies, pine forest, 6000–7000 ft., *Gentry* 6181.

PELTODON

P. PUSILLUS Pohl. BRASIL: MATTO GROSSO: Braco, Rio Arinos, *Baldwin* 3064.

SATUREJA

S. ELLIPTICA (R. & P.) Briq. Add as a synonym *Gardoquia pilosa* Gray, *Proc. Am. Acad.* 5: 341. 1862. The TYPE is at the U. S. National Herbarium. According to E. P. Killip, to whom I am indebted for this note, Gray's species is listed in the Index Kewensis as coming from the Fiji Islands although in fact collected at Baños in Peru.

S. GUATEMALENSIS Standl. GUATEMALA: DEPT. HUEHUETENANGO: La Sierra (Tujimach); across river from San Juan Atitan, Sierra de los Cuchumatanes, 2500–2900 m., *Steyermark* 52014. Suggests a shade form, just as the following suggests a sun form: Trail between Todos Santos and San Juan Atitan, Sierra de los Cuchumatanes, 2600–2700 m., *Steyermark* 51957. The differences in aspect are extreme.

S. BOLIVIANA (Benth.) Briq. The typical form of this widespread species is glabrate, with narrowly obovate entire leaves; the stems appear to be strict. This form ranges from Peru to Tucuman. In Argentine, ranging into adjacent Bolivia, is a variant [var. *tarijense* (Wedd.) Epl.] in which the habit is more lax, the leaves notably larger, rhomboid-elliptical and more or less serrulate. These forms intergrade. Now, in Peru, appears what seems to be a variant of this latter in which the branchlets, instead of being minutely hirtellous with more or less spreading hairs are definitely pubescent with downwardly curled hairs; the leaves also are cinereous and minutely hirtellous. The flowers are fasciated on short axillary branchlets. It is represented by *Metcalf* 30707, collected in Peru, Dept. Puno, Prov. Sandia, 7 km. on road from Cuyocuyo to summit, at 3600 m. *Metcalf* 30435, collected in the same province 2–6 km. south of Limbani, is intermediate, and *Metcalf* 30687, collected 8 km. from Chucinto, is typical of the species. The extremes are so unlike as to suggest a specific difference.

HEDEOMA

H. COSTATUM Gray. TEXAS: HUDSPETH COUNTY: Upper end of Victoria canyon, Sierra Diablos, *Waterfall* 4813.

H. DRUMMONDI Benth. TEXAS: HUDSPETH COUNTY: 1 mile west of McAdoo Ranch near Victoria canyon, Sierra Diablos, *Waterfall* 5357.

SALVIA

S. SUMMA A. Nels. What appears to be this species, described from S. E. New Mexico, (or perhaps a form of *S. Henryi* Gray) has been collected in

the Sierra Diablos, Hudspeth Co., Texas, by Waterfall (No. 5375). The specimen is inadequate. The distribution and range of variation of the group of species to which *S. summa* is allied (*S. Roemeriana*, *S. Henryi*, *S. Davidsoni*, and an undescribed species from N. E. Mexico) are imperfectly known. Much more material than is available is needed for study.

2. *S. OCCIDENTALIS* Sw. GUATEMALA: DEPT. RETALHULEU: vicinity of Retalhuleu, 240 m., *Standley* 88626.

9. *S. PINGUIFOLIA* W. & S. MEXICO: CHIHUAHUA: Canyon de las Varas, Santa Clara Mts., 5675 ft., *Shreve* 9012.

32. *S. TERESAE* Fern. MEXICO: MEXICO: Temascaltepec, Temascaltepec, 1750 m., *Hinton* 1117. Same, TENERIA, 2000 m., *Hinton* 952. Same, Mina de Agua, *Hinton* 16075.

41. *S. LAVANDULOIDES* Kunth. GUATEMALA: DEPT. HUEHUETENANGO: top of Cerro Chemalito, Sierra de los Cuchumatanes, 3.5 mi. West of Santa Eulalia, 3100-3150 m., *Steyermark* 49923. A form with minute appressed silvery pubescence which occurs throughout the range of the species (Michoacan; *Hinton*; Chiapas, *Matuda*).

42. *S. AGNES* Epling. MICHOACAN: Cloud forest, Mun. Tancitaré, 10,500 ft., *Leavenworth and Hoogstraal* 4036. The annual stems arise from a tuberous woody caudex.

57. *S. CORRUGATA* Vahl. ECUADOR: BOLIVAR: San Juan to Guaranda, 3600 m., *Haught* 3281.

59a. *S. LEUCOCCHLAMYS* Epling. GUATEMALA: DEPT. HUEHUETENANGO: dry southwest-facing slopes of Sierra de los Cuchumatanes, between Chiantla and Patio de Bolas, 2100-2500 m., *Steyermark* 48230; 48231. The second specimen cited is similar to the type, collected in the same region; the first is much less densely tomentose. The petioles may be as much as 1 cm. long. Mountains west of Aguacatán on road to Huehuetenango, 1950 m., *Standley* 81185.

65. *S. OREOPOLA* Fern. A plant which may be referable to this species has been collected by *Hinton* (No. 16069) at Amoloya, Sultepec, State of Mexico.

103. *S. PICHINCHIENSIS* Benth. ECUADOR: BOLIVAR: Balsapampa, 2500 m., *Haught* 3301.

107a. *S. camporum* Epling, sp. nov. (17. *Macrostachya*.) Herba perennis altitudine ad 1 m. caulibus glanduloso-villosis sordidis sat crassis; foliorum laminis cordatis, crassiusculis ad 10 cm. longis (? et ultra), petiolatis, in apice acuminatis, serrulato-crenatis, pagina superiore dense villosula, inferiore albo-tomentosa molle; floribus verisimiliter oppositis in spicis brevibus confertis bracteis deciduis (semper?) bidentatis subtentis; calycum extus glanduloso-villosorum labia superiore (semper?) tridentata, quam inferior longiore, 7-venis at tamen tribus prominulis, dentibus inferioribus deltoideis, tubo labiam superiorem subsequente, 3.5 mm. longo, in maturitate vix aucto ut videtur lateraliter compresso; corollarum cyanearum tubo recto 11 mm. longo, intus nudo tamen ut videtur lateraliter bisaccato; labia superiore acuto, inferiore in toto non viso tamen verisimiliter quam superior longiore et patente; staminibus e tubo 15 mm. exsertis paulo supra medium positiss, gubernaculo in basi deltoideo-ampliato; stylo glabro, ramo superiore brevior.

PERU: AMAZONAS: Prov. Chachapoyas, 2 km. north of Chachapoyas, 2350 m., in any open grassland, red clay and rocky soil. *Metcalf 30805* (USNH, TYPE).

108. *S. MACROPHYLLA* Benth. PERU: DEPT. HUANCAYELICA: Salcabamba, 3300 m., *Stork and Horton 10294*.

113. *S. SCUTELLARIOIDES* Kunth. COLOMBIA: CORDILLERA OCCIDENTAL: vertiente occidental cerca del filo divisorio entre el Depto. de El Valle y La Intendencia del Chocó, al norte de Albán, 2100 m., *Dugand and Jaramillo 3051*.

118. *S. MENDAX* Epling. GUATEMALA: DEPT. EL PROGRESO: between Finca Piamonte and top of Montaña Piamonte, along Joya Pacayal, 2500-3000 m., *Steyermark 13713*.

119. *S. PATENS* Cav. MEXICO: MEXICO: Sultepec, Almoloya. *Hinton 16072*. The calyces are small, resembling those of *S. mendax* of Guatemala; for the rest, this specimen seems referable here.

138. *S. RUBESCENS* Kunth. COLOMBIA: ANTIOQUIA: San Pedro. *Bro. Tomas 1004*.

139a (262). *S. (LONGIPES) MADRENSIS* Seem. MEXICO: SINALOA: Quebrado de Mansana, Sierra Surotato. Oak forest, 4000-4500 ft. *Gentry 6411*. Previously known only from the type, collected by Seemann in the "Sierra Madre" of N. W. Mexico, and assigned by me to section *Dusenostachys* to the species of which it bears resemblance. This specimen, however, permits a more satisfactory examination of the corollas which indicate its reference to the following newly erected section:

Sect. 29a. *Longipes* Epling, sect. nov

Herbae perennes sat crassae altitudine 1-2 m., foliis amplis ovato-cordatis petiolis sat longis elatis; floribus plerumque 12 et ultra in verticillastris in spicis interruptis elongatis speciosis flavidis dispositis; pedicellis gracilibus calyces subaequantibus vel longioribus; bracteis deciduis; calycum labiis subaequilongis, superiore 7-venis; corollis pallide flavidis intus nudis, labiis subaequilongis; staminibus inter tubi medium et fauces positis, in galea inclusis; gubernaculo ad medium dente retrorso ornato; stylo utrimque pubescente, ramo postico longiore. Plantae Mexicanae.

This newly proposed section bears a general resemblance to the sections *Rubescentes*, *Ampellophyllae* and *Dusenostachys*. It differs from all of them in the details of structure of the calyx and corolla. In the general key it would be sought near *Secundae*. The key (p. 11, line 4) should therefore be amended to read as follows:

DD. Staminum gubernacula vel integra vel ad connexum in dentem parvum extensum vel retrorsum ornata. E. Stamina inter corollae tubi medium et fauces posita (vide etiam *Albolanatas* et *Rubescentes*). F. Pedicelli 2-6 rarius 10 mm. longi; plantae austro-americanae, *S. Dugesiana* excepta.

91 *Secundae*. FF. Pedicelli plerumque 10-20 mm. longi; plantae sinaloenses floribus flavidis. 29a. *Longipes*.

154. *S. HAENKEI* Benth. *Soukup 400* labelled as coming from Puno, Peru, was in fact collected at La Paz, Bolivia (fide E. P. Killip).

172. *S. CALOCALICINA* Briq. COLOMBIA: COMISARÍA DEL PUTUMAYO: alta cuenca del río Putumayo en El Valle de Sibundoy extremo E., junto a San Francisco, 2200 m., *Cuatrecasas 11539*.

173. *S. CINNABARINA* M. & G. GUATEMALA: DEPT. EL PROGRESO: Hills between Finca Piamonte and slopes southeast, 2400–2500 m., *Steyermark 43460*.

174. *S. ELEGANS* Vahl. Add as a probable synonym *S. rutilans* Carr. in Rev. Hort. 251.1873. Specimens from the Cambridge Botanic Garden, thus named by Gray and received by me from Prof. L. H. Bailey are referable to *Salvia elegans*.

189. *S. MOCINOI* Benth. GUATEMALA: Jutiapa: Hills between Jutiapa and Plan de Urrutia, 900–1200 m., *Standley 75469; 75618*. Between Jutiapa and Las Tunas, 850–900 m., *Standley 76292*. Jutiapa, 850 m., *Standley 75693*. Escuintla: Wooded barranca of Rio Burrion, northeast of Escuintla, 720 m., *Standley 89567*.

219. *S. RUPICOLA* Fern. MEXICO: 175 km. north of Mexico City (presumably on the international highway), 16.VII.1940, *R. D. Northcraft 6*. Hidalgo: Tasquillo, 8000 ft., 17.VII. 1940, *Hitchcock and Stanford 7255*. A shrub to 1.5 m. or more, the leaves 1–3 cm. long, rounded or subcordate at the base, the petioles mostly 8–15 mm. long. The type of this species (*Purpus 431*) was evidently a small leaved form. However, Rose's specimen from the same locality clearly connects the above-cited specimens.

224a. *S. CAPILLOSA* Epling. MEXICO: MEXICO: Sultepec, Amoloya, *Hinton 15399*. Apparently this, but the leaves smaller and less cordate, the flowers smaller and the spikes more dense than the plants of Michoacan.

225. *S. URICA* Epling. GUATEMALA: DEPT. ZACAPA: Sierra de las Minas, *Steyermark 12935; 12115*.

244. *S. AZUREA* Michx. ex Lam. subsp. *TYPICA* Epling. TEXAS: JASPER COUNTY: Near Jasper, *Lundell and Geiser 11811*. NEWTON COUNTY: East of Newton, *Lundell & Geiser 11889*.

279. *S. COMPACTA* Kunze. PANAMA: El Volcan, Rio Chiriqui Viejo. *G. White 11*. Probably an extreme form of *S. polystachya*.

294. *S. GRACILIS* Benth. GUATEMALA: DEPT. HUEHUETENANGO: above San Juan Ixcay, Sierra de los Cuchumatanes, 2400 m., *Steyermark 50082*. The flowers of this section (*Carneae*) are ordinarily rose-purple and the calyces are often similarly colored, as in *Skutch 1090* from the same locality as the above-cited specimen. However, Skutch reports the "throat white with a rose-magenta line down center." Steyermark describes the corolla of his specimen as follows: "Lower lip of flower white with orchid-rose-colored margin; upper lip of corolla whitish with pale, orchid-colored tip." He describes *No. 50084* from the same locality as "calyx purple; flower with more orchid-rose color," and *No. 51879* as a "rich orchid color, the lower lip with a patch of white in upper center."

309. *S. CAUDATA* Epling. Nuevo León. Villa de Santiago, near Horse-tail Falls, *Leavenworth 809*. The bracts may be fairly early deciduous, the calyces as much as 11.5 mm. long at anthesis and scarcely larger at maturity, and the corolla tube may be 13 mm. long.

319. *S. MYRIANTHA* Epling. GUATEMALA: DEPT. EL PROGRESO: Sierra de las Minas, *Steyermark 13651*.

319a. *SALVIA PSILOPHYLLA* Epling. PANAMA: CHIRIQUÍ: Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m., *Woodson and Schery 452*.

According to the collection data, this specimen came from a small tree to 3 m. in height.

329. *S. LONGIMARGINATA* Briq. VENEZUELA: ARAGUA: Parque Nacional, near Rancho Grande, 800–1000 m., forest, *Killip 37125*.

336. *S. XALAPENSIS* Benth. MEXICO: MEXICO: Tlaxcaltepec, *Hinton 16073*.

343. *S. FLACCIDA* Fenzl. GUATEMALA: DEPT. IZABAL: Cerro San Gil, 1200–1300 m., *Steyermark 41948*.

352. *S. PANSAMALENSIS* J. D. Smith. GUATEMALA: DEPT. HUEHUETENANGO: Cerro Chiblac, between Finca San Rafael and Ixcán, Sierra de las Cuchumatanes, 1200–2000 m., *Steyermark 49156*. Previously known only from the type, collected in Alta Vera Paz.

Sect. 70a. *Steyermarkia* Epling, sect. nov.

Frutices grandes insignes ramulis et foliis utrimque glaberrimis; foliis lanceolato-ellipticis, utrimque angustatis, coriaceis, breviter petiolatis; floribus magnam partem 6 (rarius 12) in glomerulis, in spicis interruptis sat confertis dispositis, bracteis insignibus purpureis subcoriaceis attenuatis modo hamatis modo sigmoideis deciduis subtentis; calycum purpureorum labia superiore 7-venis acuminata quam inferior longiore; corollarum tubo complanato ad basim papillis binis longioribus transversis ornato, ventricosus, labia superiore galeata inferiorem subaequante; staminum inclusorum gubernaculo ad medium infra connexum in dentem parvum producto; stylo ad apicem piloso, ramo antico brevior obtuso vel truncato, postice attenuato; nuculis nigris, hilo obscuro.—The flowers of this proposed section are scarcely different from those of *Cardinales*, and the bracts are similar in conformation. But the habit of foliage is so strikingly different and the whole aspect of the plant so unique, that it seems preferable to assign it to a separate section, which it is a pleasure to name in honor of Dr. Julian A. Steyermark, whose explorations in Guatemala have produced not only this remarkable species, but numerous others.

The key to the sections (p. 12, line 11) should be modified to read as follows:

MM. Corollarum tubi intus papillis binis ornati modo invagnati modo integri N. Folia sat membranacea, ovata vel cordata, petiolis 1–10 cm. longis elata 70. *Cardinales*. NN Folia coriacea, lanceolata-elliptica, glaberrima, petiolis 3–8 mm. longis elata. 70a. *Steyermarkia*. LL Corollarum labia . . .

394a. *S. grandis* Epling, sp. nov. Frutex grandis altitudine ad 7 m. (!) ramulis glaberrimis, internodiis quam folia multo brevioribus; foliorum laminis lanceolato-ellipticis, 8–12 cm. longis, 1.5–3 cm. latis, coriaceis, venulosis, acute serrulatis, paginis ambabus glaberrimis, inferiore pallidiore; petiolis 3–8 mm. longis; floribus saepius 3 rarius 6 in bracteorum insignum axillis dispositis, in spicis interruptis villosis 10–20 cm. longis instructis; bracteis subcoriaceis, purpureis, attenuatis, caniculatis, hamato-recurvis et frequenter sigmoideis 1.5–3 cm. longis, deciduis, extus purpureo-villosis; calycum purpurearum florentium tubis 7–8 mm. longis, costatis, extus purpureo-villosis, in maturitate paulo auctis, labiis maturis 6–7 mm. longis, acuminatis; corollarum roseo-purpurearum tubis 16–17 mm. longis, labiis subaequilongis, 6 mm. longis; nuculis nigris.

GUATEMALA: DEPT. EL PROGRESO: hills between Finca Piamonte and slopes southeast, 2400-2500 m., 4.II.1942, *Steyermark 43456*; hills north of Finca Piamonte, between Finca Piamonte and summit of volcan Santa Luisa, 2400-3333 m., 5.II.1942, *Steyermark 43482*; between Calera and summit of volcan Siglo, 2000-3300 m., 21.I.1942, *Steyermark 43047* (TYPE, Univ. Calif., Los Angeles). DEPT. ZACAPA: between Loma El Picacho and Cerre de Monos, Sierra de las Minas, 2000-2600 m., 16.I.1942, *Steyermark 42768*.

405. *S. LEUCOCEPHALA* Kunth. ECUADOR: CHIMBORAZO: Sibambe, 1900 m., mostly near streams, *Haught 3319*.

410. *S. DOMBEYI* Epl. PERU: PUNO: Prov. Sandia, near Limbani, 3200-3450 m., *Metcalf 30476*.

Sect. 79a. **Weberbaueria** Epling, sect. nov.

Frutices foliis amplis ovatis et cordatis villosis; floribus tribus in verticillastris bracteis deciduis amplis subtentis in spicis interruptis dispositis; calyceum labia superiore 5-7 venis; corollarum violacearum tubo 42-45 mm. longo superne gradatim ampliato sat crasso, intus ad basim papillis 2-4 ornato et lateraliter bisaccato; labia inferiore patente amplo quam superior galeata longiore; staminibus in labia superiore inclusis, gubernaculo integro; stylo glabro, ramo superiore longiore. Plantae peruvianae.

413a. (olim 411) *S. SCANDENS* Epl. PERU: PUNO: Prov. Sandia, near Limbani, 3200-3450 m., *Metcalf 30489*. The type, collected by Weberbauer in Cuzco near Marcapata was noted by him as scandent; this specimen was noted as a shrub 2 m. high. Because the flower parts of the type were inadequate for an accurate description, the species can now be more fully characterized and classified. Because of the papillate corolla tube, the longer lower lip of the corolla and its violet color, it seems preferable to distinguish it from *Longiflorae* to which it was originally assigned by me. *Weberbaueria* would accordingly be sought in the general key on page 11 line 27 under 79. *Longiflorae*, which can be changed to read 79a *Weberbaueria*.

418. *S. PALMERI* Gray. MEXICO: SONORA: Canyon on the northeast side of Sierra Batuc, 10 mi. from Matape between Matape and Batuc, 3100 ft., *Wiggins and Rollins 115*.

435. *S. TORTUOSA* Kunth. ECUADOR: PROV. COTOPAXI: Between Pilalao and Macuchi, 2500 m., *Haught 2957*. Both the typical form with densely wooly calyces and var. *detonsa* Epl., with glabrous calyces, are represented.—Comisaria del Putumayo: alta cuenca del río Putumayo en El Valle de Sibundoy extremo E., junto a San Francisco, 2200 m., *Cuatrecasas 11560*. Known previously only from Ecuador. The upper lip of the calyx of this species is sometimes clearly 5-nerved, as in this specimen.

443a. *S. areolata* (*Purpureae*) Epling, sp. nov. Frutices altitudine ad 1 m. ramulis dense tomentosis; foliorum laminis coriaceis 2.5-3.5 cm. longis, ovatis, in apice obtusis, in basi rotundatis, marginibus obscure serrulatis, pagina superiore rugoso-areolata, areolis molliter hirsutis, inferiore mollissime et densissime tomentosa in siccis rufa; petiolis ad 1 cm. longis; floribus 3-6 in verticillastris inter se ad 2 cm. distantibus in spicis interruptis 5-10 cm. longis dispositis, bracteis deciduis acuminatis molliter hirsutis

subtensis; calycibus florentibus 8 mm. longis, extus tomentosis, in maturitate paulo auctis latoribus, pedicellis 2-3 mm. longis elatis; corollarum purpurearum tubo 10 mm. longo.

GUATEMALA: HUEHUETENANGO: Between Chémal and Calaveras, Sierra de los Cuchumatanes, 2800-3700 m., 9. VIII. 1942, *Steyermark 50388*. "With Agave. on southern rocky rim on summit of mountains. Leaves very rugose both sides, dull deep blue-grey-green above, buff-greyish beneath." (FM, TYPE). Seems closest in most ways to *S. sordida*.

443b. *S. sparsiflora* (Purpureae) Epling, sp. nov. Frutices altitudine 1 m. et ultra ramulis pilis brevibus recurvis vel retrorsis hirtellis; foliorum laminis coriaceis in specimine suppetente 3-4 cm. longis, ovato-ellipticis, in apice obtusis vel breviter acuminatis, in basi ad petiolos 5-6 mm. longos rotundato-angustatis, marginibus serrulatis, pagina superiore et inferiore praesertim ad venas hirtella; floribus paucis 1-3 in verticillastris inter se 3-6 mm. distantibus in spicis interruptis 3-5 cm. longis dispositis, bracteis caducis subtensis; calycibus florentibus 7-8 mm. longis extus sparse hispidulis, in maturitate paulo auctis latoribus, pedicellis 5 mm. longis elatis; corollarum purpurearum tubo 12 mm. longo, infra papillas leniter constricto superne plus minusve ventricosus.

GUATEMALA: HUEHUETENANGO: Between Los Palmas and Chaculá, Sierra de los Cuchumatanes, 1400-1600 m., 1. VIII. 1942, *Steyermark 51740* (FM, TYPE). Suggests *S. Cuatrecasana* in many ways and, with the preceding species, is more like the South American representatives of this section than those of North America.

443c. *S. Cuatrecasana* Epling, sp. nov. Frutex ramulis pilis longioribus extensis sparse villosis, internodiis quam folia brevioribus; foliorum laminis subcoriaceis ellipticis, interdum ovalibus, plerumque 3-4 cm. longis et 1-2.5 cm. latis, in apice obtusiusculis, in basi angustatis, serrulatis, pagina superiore sparse appresso-hirsuta, inferiore pallidior fere glabra; petiolis 3-4 r. m. longis; floribus in spicas 3-6 cm. longas confertis; calycibus florentibus saepius purpureis 9-10 mm. longis, laciniis breviter acuminatis, extus glabris, venis prominulis; corollarum purpurearum tubo 12-13 mm. longo, labia inferiore modo quam superior breviori modo paulo longiore; staminum jugo 9 mm. longo.

COLOMBIA: DEPT. BOYACÁ: Cord. Oriental. Quebrada de Becerra al noroeste de Duitama, paramos entre bosque, 2970-3300 m., 4.VIII.1940. *Cuatrecasas 10407* (USNH, TYPE). In habit and aspect, this plant suggests *S. sphacelioides* of section *Angulatae* and also resembles *S. Kellermanni* of section *Maxonia*. However, the flower color and structure, while not wholly typical of section *Purpureae*, suggest its reference here.

ERIOPE

***E. angustifolia* (Hypenioideae) Epling, sp. nov.** Herba perennis altitudine ad 1 m. caulibus erectis ut videtur strictis et verisimiliter e caudice lignoso productis, nisi inter flores nisi ad radice utrimque glaberrimis et glaucis, internodiis elongatis et per insectorum larvas tumidis; foliis infimis et mediis ut videtur deciduis, supremorum laminis linearibus vel linearo-ellipticis 5-8 cm. longis, 3-6 mm. latis, sessilibus, acutis, serratis, utrimque

glabris; paniculorum amplorum ramis subdivaricatis gracilibus, internodiis modo glabris et glaucis modo dense et minute glandulosis, etiam pilis longioribus extensis hispidis; floribus inter se 5–10 mm. distantibus, pedicellis gracilibus 4–5 mm. longis elatis; calyceibus florentibus 3 mm. longis, in maturitate vix 5 mm. longis; corollis non visis.

BRASIL: GOYAZ: In campo, Serra de Cipo, Santa Luzia, 20.IX.1937. *Barreto 912A* (Field Mus., TYPE).

E. (?) *TEUCRIODES* St. Hil. BRASIL: GOYAZ: In campo pedregoso, Serra de Cipó, Santa Luzia, 25.XI.1938, *Barreto 8605*.

E. *FILIFOLIA* Benth. BRASIL: MINAS GERAES: In campo arenoso, Arranca Rabo, Diamantina, 3.XI.1937, *Barreto 9383*.

E. *trichopes* (Crassipedes) Epling, sp. nov. Herba perennis diffusa altitudine 20–40 cm. ramis subsimplicibus gracilibus e caudice lignoso ascendentibus, et ramulis brevibus ascendentibus hirtellis et pilis crassiusculis conspersis; foliorum laminis parvis quam internodia multo brevioribus, rhomboido-ovatis, sat tenuibus, 4–6 mm. longis, pro rata grande et irregulariter dentatis, pilis crassiusculis conspersis; racemis foliolosis 10–20 cm. longis; floribus inter se 10–20 mm. distantibus, pedicellis tenuibus 12–15 mm. longis elatis; calyceibus florentibus vix 1.5 mm. longis, in maturitate duplo longioribus; corollarum tubo 2 mm. longo.

CUBA: Isle of Pines, vicinity of San Pedro in pinelands, 15,171,1916. *Britton, Wilson and Selby 14169* (TYPE, N. Y. Bot. Gard.; isotype U.S.N.H.).

HYPTIS

H. (*Minthidium*) *mixta* Epling, sp. nov. Herba verisimiliter perennis caulis molliter pubescentibus, internodiis sat elongatis; foliorum laminis ovatis, 3.5–4.5 cm. longis, acutis, in basi rotundato-angustatis, irregulariter serratis, pagina superiore hirtella, viride, inferiore molliter pubescente, canescente; glomerulis hemisphaericis 19–12 mm. diametro in spicis submoniliformibus dispositis, infimis inter se 2–3 cm. distantibus, pedunculis 2–5 mm. longis elatis, bracteis paucis subfoliosis, parvis ovato-lanceolatis subtentis; calycum florentium tubo vix 1.5 mm. longo, in maturitate 4.5 mm. longo, fere 2 mm. diametro, dentibus inequalibus brevibus linearibus vix 1 mm. longis; corollarum albarum tubo 1.5 mm. longo, nuculis dorsaliter gibbis duobus tenuibus ornatis.

MEXICO: OAXACA: Tuxtepec, Chiltepec and vicinity, 20 m., VII.1940–11.1941, *Martinez-Calderon 251* (TYPE, U.S.N.H.).

A species which, while referable to this section by reason of the calyx and flower habit, has calyx teeth which are suggestive of those of sections *Polydesmia* and *Eriosphaeria*. It is perhaps most nearly allied to *H. scandens*.

H. *SCANDENS* Epling. GUATEMALA: DEPT. PETEN: semi-chaparral area, across river from Sayaxché, 50 m., *Steyermark 16305*. Previously known only from the type, collected at El Paso and described by the collector as a "woody vine in *acahual*." This specimen is described as a bushy herb 5 feet tall.

H. (Cyrta: *Paludosae*) *microsphaera* Epling, sp. nov. Herba inamoena altitudine 1.5 m., caulis verisimiliter paucis ascendentibus pilis minutis

ascendentibus et plus minuse appressis hirtellis, internodiis elongatis et folia superantibus; foliorum laminis ovatis vel rhomboideo-ovatis, 1.5–3 cm. longis, superiorum subsessilibus, inferiorum ad petiolos 2–4 cm. longos cuneato-angustatis, in apice obtusis, in basi rotundato-cuneatis, crenato-serratis, utrimque tenuiter hirtellis, fere glabris; glomerulis in paniculis bracteatis dispositis, globosis, densis, 5–10 mm. diametro, pedunculis gracilibus 1–1.5 cm. longis elatis, bracteis appresso-hirtellis fere glabris subtentis; calycibus florentibus vix 3 mm. longis, glandulis sessilibus dense obsitis, nullomodo hirtellis, dentibus quam tubus brevioribus, obtusis, tubis maturis vix 3 mm. longis; corollarum albarum tubo vix 3 mm. longo; nuculis ovoideis, .7 mm. longis.

VENEZUELA: Bajos del rio Tigre, 1230 m., en Cristovero, ESE de Santomé Anzoategui, 19.XII.1940, *Pittier 14597* (TYPE, Herb. Nac. Venezuela).

H. SINUATA Pohl. GUATEMALA: DEPT. RETALHULEU: Along Rio Ocosito, east of Retalhuleu, 300 m., *Standley 88279*. Dept. Escuintla. Along or near Rio Michatoya, s.e. of Escuintla, 250–300 m., *Standley 89079*.

H. SAVANNARUM Briq. GUATEMALA: ALTA VERA PAZ: Bogs near Santa Cruz along road to San Cristobal, 1350 m., *Standley 92728*.

H. D.LATATA Benth. VENEZUELA: BOLIVAR: Rio Paragua, near Chorrera de Aguacante, 260 m., sabanas, *Killip 37559*.

H. ATRORUBENS Poit. MEXICO: OAXACA: Tuxtepec, Chiltepec, and vic., 20 m., in llanos, *Martinez-Calderon 366*.

H. PULEGIOIDES Pohl. VENEZUELA: COJEDES: sabanas south of San Carlos, 14.XI.1940, *Chardon 218*.

H. RECURVATA Poit. GUATEMALA: DEPT. RETALHULEU: Along Rio Ocosito, west of Retalhuleu, 300 m., *Standley 88268*. Vicinity of Las Delicias, s. of Retalhuleu, 200 m., *Standley 88048*.

H. CONFERTA Pohl. var. ANGUSTIFOLIA Benth. VENEZUELA: BOLIVAR: Rio Paragua near Chorrera de Aguacante, 260 m., sabanas, *Killip 37556*. Between Ciudad Bolivar and El Cristo, 100–300 m., sabanas, *Killip 37634*.

H. INTERMEDIA Epling. GUATEMALA: DEPT. HUEHUETENANGO: Between Ixcán and Rio Ixcán, Sierra de los Cuchumatanes, 150–200 m., *Steyermark 19314*.

H. VILIS Kunth & Bouche. VENEZUELA: DISTRITO FEDERAL: El Junquito, 1925 m., forest, *Killip and Rohl 37200*.

H. LANTANAEFOLIA Poit. PERU: PUNO: Prov. Sandia, near Pajonal, 1000–1300 m., *Metcalf 30618*.

H. UNCINATA Benth. PERU: PUNO: Prov. Sandia, 2 km. N. of Chamacani, 2500 m., *Metcalf 30553*. Same, 2–6 km. from Oconeque, 1800–2100 m., *Metcalf 30580*. The latter is described as a straggling vine.

COLEUS

C. ATROPURPUREUS Benth. COLOMBIA: INTENDENCIA DEL CHOCÓ: Quibdó. Río Atrato; alt. 60 m., *Archer 1795*. El Valle. Dense forest near highway bridge over Río Dagua, about 20 km. east of Buenaventura, 40 m., *Killip and Garcia 33319*. VENEZUELA: ARAGUA: Parque Nacional; near Rancho Grande, 800–1000 m., forest, *Killip 37121*.

So far as I am aware this species has not heretofore been reported from the New World. The genus itself is generally considered to be wholly Old World, only *C. Blumci* sometimes being picked up in the American tropics as an escape. When Archer's specimen gathered in 1931, first came to me, I assumed that it was a stray. But Killip's collections, made in 1939 and 1943, suggest the possibility that the species is at home in northern South America. However, Mr. Killip writes, "I suppose it is an introduction, though it occurs in out of the way places. I have found it in wet places along a railroad or in clearings in forests." The Archer specimen was identified at Kew, presumably through the kindness of Mr. Sandwith.

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CHROMOSOME NUMBERS IN VACCINIUM AND
RELATED GROUPSGEORGE M. DARROW, W. H. CAMP, H. E. FISCHER,
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Today, as never before, the plant breeder interested in the development of new horticultural material, and the taxonomist concerned with the delimitation of species, have a common meeting ground. To do effective work, the plant breeder must have considerable knowledge of the cytogenetic systems of the group he is seeking to improve; and the taxonomist must clearly understand these same basic phenomena and the role they have played in speciation before his interpretation of the group can result in an effective nomenclature. This paper is one of a series based on a cooperative effort to solve the problems involved in the horticultural development and taxonomic interpretation of the North American blueberries (*Vaccinium* spp.), cranberries, and related groups.

The early activity in the breeding of blueberries sponsored by the United States Department of Agriculture was carried on by F. V. Coville and O. M. Freeman; since 1938, the senior author has been in charge of the work. It was evident from the beginning that barriers were present to the free crossing of certain species, while others might be hybridized with ease. This was not satisfactorily explained until certain findings were reported by Coville and by Longley in companion papers. In his report, Longley (11) announced that three chromosome groups were to be found in blueberries, namely, diploid, tetraploid, and hexaploid. As a result of his breeding work, Coville (4) announced that the members of the diploid and tetraploid groups would not hybridize, but that species within any chromosome group were interfertile. The importance of these facts was immediately obvious to those interested in the horticultural development of the blueberry. More recently, consideration of this and additional information has resulted in a systematic and phyletic reinterpretation of certain segments of the genus *Vaccinium* (1, 2); also, they have indicated the need for a clarification of the principles underlying speciation and related problems (3).

Once it was clearly established that a knowledge of chromosome number was essential in any large breeding program in blueberries, steps were taken

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to speed up this phase of the work. Various reports in the literature indicated that it might be possible to distinguish between the different levels of polyploidy more rapidly by means of techniques other than those usually employed in the direct counting of chromosomes. In the beginning, these methods offered encouragement for it was noted that, in general, stomate size increased and stomate frequency decreased from the diploids through the tetraploids and to the hexaploids (15, 14). Also, there was an apparent increase in the size of pollen grains correlated with a polyploidal condition. However, as the work progressed, aberrancies were noted. They were such that complete confidence could not be placed in these types of examinations.

Since these methods have been successful in other genera and appear to be effective in restricted portions of our material, there must be some reason for their lack of more general application in *Vaccinium*. Briefly, it is our opinion that the extreme variability of the group, together with the complicated line of descent of certain of its segments, has disturbed what, otherwise, might be an expected morphological pattern in the development of the polyploids.

Morphologically, some of the basic, diploid blueberry species are so different that one is almost tempted to consider the group to have more than one line of descent; certainly, if they have diverged from a common ancestral stock, it must have been fairly early in the Tertiary. On the other hand, our work has shown that these divergent elements—in various combinations—have been the source of the allopolyploid species which it contains. Thus, in a broad study of the genus *Vaccinium*, we are faced with the problems of both divergent and convergent evolutions. The over-all picture of the group, then, is one with a more-or-less reticulate type of speciation (10, Chapter 6).

Had we been dealing only with simple series of autopolyploids (some of which exist in *Vaccinium*), the examination of stomate size and frequency, or the relative size of pollen grains, might serve adequately to indicate whether a given plant was diploid, tetraploid, or hexaploid. But the foregoing brief discussion of conditions within the genus, together with the fact that our findings in both hybrid and allopolyploid complexes could not be completely relied upon, led us to reject such a method. Instead, it seemed safer to rely on a direct examination of the chromosomes to determine their number. Several of the standard cytological methods have been used.

Table 1 is an annotated list of the results of this phase of the work,² together with additional information from reports in the literature. In some instances the material included here was reported as belonging to other genera; in every case these are integral parts of the large complex of the

² A partial abstract of this report was previously published (5). Certain corrections and additions have been incorporated in the present paper.

TABLE 1. Summary of known chromosome numbers in blueberry species and varieties of eastern North America

A. Diploid species (2n = 24)	Variety or description	Source of material
<i>V. angustifolium</i> Aiton ^a	Lowbush, glabrous, blue fruit	Arnold Arboretum, Jamaica Plain, Mass.
do	do	Buddtown, N. J.
<i>V. atrococcum</i> (Gray) Heller ^b	Highbush, pubescent, black fruit	Orono, Maine
do	do	Arnold Arboretum, Mass.
do (11 plants)	do	Beltsville, Md.
do	do	Cedartown, Ga.
do	do	Brunswick, Ga.
do	do	Jackson, Tenn.
<i>V. cacsariense</i> Mackenzie ^a	Highbush, glabrous, blue fruit	Beltsville, Md.
do	do	Brunswick, Ga.
<i>V. myrtilloides</i> Michx. ^b	Lowbush, pubescent, frosty blue fruit	Adirondack Mountains, N. Y.
do	do	Arnold Arboretum, Mass.
<i>V. darrowi</i> Camp ^a	Lowbush, evergreen	Crestview, Fla.
<i>V. elliotii</i> Chapman ^a	Highbush, cassena leaved	Ivanhoe, N. C.
do	do	Munson, Fla.
do	Red flowered, tall	do
<i>V. margarettae</i> Ashe ^a	Lowbush, pubescent, dark fruit	Edwardsville, Ala.
<i>V. pallidum</i> Aiton ^c	Lowbush, glabrous, blue fruit, dryland type	Beltsville, Md.
do	do	Pickens, S. C.
<i>V. tenellum</i> Aiton ^a	Lowbush, glandular, black fruit	Ivanhoe, N. C.
<i>V. vacillans</i> ^c (2 plants)	Lowbush, glabrous & puberulent, blue fruit	New York Botanical Garden, N. Y.
<i>V. vacillans</i> × <i>atrococcum</i> ^a	Halfhigh, very pubescent, dark fruit (from wild)	do
<i>V. vacillans</i> × <i>cacsariense</i> ^a	Halfhigh, glabrous, blue fruit (from wild)	do
<i>V. elliotii</i> × <i>tenellum</i> (= <i>V. cuthberti</i> (Small) Uphof) ^a	Highbush, subglandular (from wild)	Brunswick, Ga.
<i>V. cacsariense</i> × <i>darrowi</i> ^a	1-2 m., evergreen (from wild)	Northern Florida
B. Tetraploid species (2n = 48)		
<i>V. lamareckii</i> Camp ^d	Lowbush, glabrous, blue fruit	Arnold Arboretum, Jamaica Plain, Mass.
<i>V. australe</i> Small ^e	Highbush, glabrous, blue fruit	Plant Industry Sta., Beltsville, Md.
do	"Hildebrand"	J. T. Bush, Toombsboro, Ga.
do	"Lanier"	do
do	"Pioneer"	Plant Industry Sta., Beltsville, Md.
do	"G. Baker #4"	do
do	"DN-76" (a Coville selection)	do
do	"Dixie"	do
<i>V.</i> (near <i>australe</i>)	On upland	Petersburg, Va.
<i>V. brittonii</i> Porter ^a	Lowbush, glaucous leaves, black fruit	Spruce Knob, W. Va.
<i>V. corymbosum</i> L. ^f	Highbush, pubescent, blue fruit	Plant Industry Sta., Beltsville, Md.
do	do	Arnold Arboretum, Mass.
do	"Kablei"	South Haven, Mich.
do	"Orvis Williams"	do
<i>V. hirsutum</i> Buckley ^h	Lowbush, leaves & fruit pubescent	Great Smoky Mountains, Tenn.
<i>V. myrsinites</i> Lam. ^b	Lowbush, glandular, evergreen	Brunswick, Ga.
do	do	Tifton, Ga.
<i>V. simulatum</i> Small ^a	Highbush, nonsuckering	Mountains, western N. C.
do	"N. C. selection"	Newlands, N. C.
<i>V. tallapuasae</i> (Cov.) Uphof ^a	"Hilleculture selection #1401"	Edwardsville, Ala.

TABLE 1—(Continued)

	Variety or description	Source of material
<i>V.</i> (near <i>tallapusae</i>)	3 feet high	Sugar Valley, Ga.
<i>V.</i> (related to <i>tallapusae</i>)	Coarse plant	Garfield, Ark.
<i>V. virgatum</i> Aiton ¹	Halfhigh (3'), glandular, black fruit	Summerton, S. C.
<i>V. lamarekii</i> × <i>hirsutum</i> ^b	Lowbush, pubescent	Plant Industry Sta., Beltsville, Md
<i>V. lamarekii</i> × <i>myrsinites</i> ^{ch}	Lowbush, evergreen	do
(<i>V. lamarekii</i> × <i>myrsinites</i>) × "corymbosum" ^{dh}	Halfhigh, leaves subsistent	do
<i>V.</i> _____ ? ⁱ	Halfhigh, glabrous, blue fruit	Arnold Arboretum, Mass.
C. Pentaploid plants (2n = 60)		
<i>V.</i> (cf. <i>virgatum</i> (4x) × <i>amoenum</i> (6x)) ^a	Highbush, suckering	Louisville, Ga.
<i>V.</i> (cf. <i>simulatum</i> (4x) × <i>constablaei</i> (6x)) ^a	do	Grandfather Mountain, N. C.
<i>V. australe</i> (4x) × <i>ashei</i> (6x) ^a	Garden hybrid	Whitesbog, N. J.
D. Hexaploid species (2n = 72)		
<i>V. constablaei</i> Gray ¹ (6 plants)	Highbush, suckering, leaves variable	Grandfather Mountain, N. C.
<i>V. amoenum</i> Aiton ^a	Highbush, suckering freely on dry land	Ogeechee River Valley, Ga.
do	do	Brunswick, Ga.
<i>V. ashei</i> Readem	"Anne"	Crestview, Fla.
do	"Baker"	Baker, Fla.
do	"Blue Boy"	Crestview, Fla.
do	"Locke"	do
do	"Long"	do
do	"Ruby"	do
do	"Suwanee"	Plant Industry Sta., Beltsville, Md.
do	"Pink bud #1"	Munson, Fla.

^a Reported here for the first time.

^b Confirms a previous report by Longley (11).

^c It is not known whether the *V. vacillans* of the Longley (11) report is to be referred to *V. pallidum* or *V. vacillans* of this paper, but probably the latter.

^d The "*V. angustifolium*" of the Longley (11) report; the nomenclatural type of *V. angustifolium* appear to belong to that population known to be diploid. *V. pensylvanicum* Mill. is an invalid name, having been applied to a non-vacciniaceae plant.

^e Although reported here for the first time, part of this material was included in *V. corymbosum* in the Longley (11) report.

^f Confirms the Longley (11) report, but excludes the material of *V. australe*.

^g Confirms a previous count of this same clone, reported by Neweomer (12) as *V. atrococcum*. Although here placed in *V. corymbosum* (on the basis of its presence in an interbreeding tetraploid community), its morphological affinities are with the Mississippi Valley *V. arkansanum*, one of the ancestors of the *V. corymbosum* hybrid complex. For details of this complex, see Camp and Gilly (3), under the discussion of the mitotic species, pp. 347-348.

^h Data taken from the Longley (11) report; for the three tetraploid hybrids here listed, see also footnote g.

ⁱ Reported here for the first time; this should not be confused with the "*V. virgatum*" of the Longley and Coville reports (4, 11), for which see footnote l.

^j Original plant labeled *V. dobbsii* Burnham, but does not exactly match the type collection. We suspect that this is a segregate of a hybrid between a glabrous phase of *V. corymbosum* and *V. lamarekii*.

^k Confirms the Longley (11) report based on the same individuals, but instead of being *V. virgatum* × *V. corymbosum*, the two parents ("rabbiteye" × "Katherine") are here interpreted to be *V. ashei* × *V. australe*.

^l Confirms the report by Longley (11) on similar material, here considered to be *V. constablaei* instead of the *V. pallidum* of that report.

^m Confirms the report of Longley (11) on then unnamed horticultural varieties belonging to this species, here considered to be included in *V. ashei* instead of *V. virgatum* of that report.

Vaccinieae and, even today, are included in *Vaccinium* by many authors. On the other hand, the group of species with which we have been most concerned—the blueberries—has been treated by several authors as a separate genus *Cyanococcus*. A discussion of the problems of generic delimitation is outside the scope of the present report.

Where possible, we have re-examined the same plants upon which the Coville and Longley (4, 11) reports were based. Much of the material has been collected by ourselves in the course of our field investigations; and some of it has been contributed by others.¹

TABLE 2. *Other species of Vaccinium in North America*

Diploid species (2n = 24)	Variety or description	Source of material
<i>V. crassifolium</i> Andr. ^a	Creeping evergreen	Atkinson, N. C.
<i>V. ovatum</i> Pursh ^b	Highbush, evergreen	Oregon Coast
<i>V. parvifolium</i> Sm. ^c	Highbush, red fruit	Northwest Coast

^a Reported here for the first time. In 1933 Small erected the genus *Herpothamnus* for this species; its affinities seem to be with other members of *Vaccinium* (sensu lat.) rather than with the blueberries.

^b Reported here for the first time. Its affinities seem to be with certain Mexican, South American, and African species.

^c Reported here for the first time on the basis of unpublished work by A. E. Longley. From its reactions with other members of the subgenus *Euraccinium*, it was previously proposed that this species would prove to be diploid (2).

DISCUSSION

From the foregoing lists, it may be noted that the findings of Longley (11) have been amply confirmed, and that *Vaccinium* and its relatives have a series of diploids, tetraploids, and hexaploids. While these reports are as yet confined to only a portion of the species of North America, Europe, and Asia Minor, a consideration of the morphological patterns of the several hundred species known to be in *Vaccinium* (sensu lat.) would lead to the conclusion that this is the general situation within this widely dispersed group. Our studies of the North American material in conjunction with the information presented here—together with intensive field investigations in critical areas—lead to the conclusion that both autopolyploidy and allopolyploidy have been responsible for the production of these polyploid populations. This has resulted in a complex phyletic pattern in the genus and has been the source of much of the present nomenclatural confusion.

¹ The following kindly furnished material, from the places indicated, for cytological studies: Karl Sax, from the Arnold Arboretum; J. M. Batchelor, from Florida and Alabama; F. L. O'Rourke, from near Glenn Dale, Md.; J. L. Murray, from Garfield, Ark.; Stanley Johnston, from Michigan; Sam Fredson, from Georgia; E. R. Morrow, from North Carolina; George Waldo, from Oregon; L. A. Fister, from Jackson, Tenn.; D. J. Crowley, from Long Beach, Wash.; F. B. Chandler, from Orono, Me.; Wm. H. Sawyer, from Lewiston, Me.

Although pentaploid plants are known, no triploids[†] have yet been found. The pentaploids are known from the wild and also have been produced freely by controlled crossings between tetraploids and hexaploids. That this is also the method of origin of the wild pentaploids seems likely for, in each in-

TABLE 3. *Additional Vaccinieae of North America, Europe, and Asia Minor*

Species or variety	Chromosome number	Source of data or material
<i>Oxycoccus</i> : ^a		
<i>O. macrocarpus</i> (Ait.) Pers. ^b	2n = 24	Eastern North America
<i>O. microcarpus</i> Turcz.	2n = 24	Europe (9)
<i>O. ovalifolius</i> (Michx.) A. E. Porsild ^c	2n = 48	Pacific Coast of North America
<i>O. quadripetalus</i> Gilib. "typical" material	2n = 48	Europe (9); Maine ^d
var. <i>microphyllum</i> (Lange) M. P. Porsild	2n = 48	do
<i>O. "gigas"</i> ^e	2n = 72	do
<i>Polycodum stamineum</i> (L.) (Greenf)	2n = 24	Eastern North America
<i>Vaccinium</i> : ^g		
<i>V. vitis-idaea</i> L. ^h	2n = 24	Europe (7)
<i>V. uliginosum</i> L. ⁱ forma <i>microphyllum</i> Lange	2n = 24	Europe (8)
forma <i>genumum</i> Herder	2n = 48	do
<i>V. arctostaphylos</i> L. ^j	2n = 48	Native of Caucasus Mountains

^a Considered by various authors to be a section or subgenus of *Vaccinium*; as *Oxycoccus*, it has received recent systematic attention by Porsild (13). A further study of this group, now in progress, will be published as part of this series of papers.

^b Periclinal and total polyploidy (4x - 48) has been experimentally induced in this species by the use of colchicine (6).

^c Reported here for the first time. The binomial based on *Vaccinium oxycoccus* var. *ovalifolius* Michx. The 3 collections studied here came from the Cascade Mountains, Grays Harbor County, and Long Beach, Wash.

^d Material collected near Lewiston, Maine.

^e As proposed by Hagerup, the binomial is invalid under the present Rules of Botanical Nomenclature. The material flowers freely, but does not set seed because of disturbances during meiosis resulting in abortive pollen.

^f Reported by Longley (11). Although the "deerberries" are a distinct group, the species of *Polycodum* are included in *Vaccinium* by many authors.

^g The species listed here under *Vaccinium* have been (or are) considered as belonging to segregate genera by various authors.

^h An essentially circumboreal species consisting of 2 fairly distinct forms, one procumbent and small-leaved, the other coarser and more erect. This may be a case of homoploid divergence, or the coarser form may yet prove to be polyploid.

ⁱ On the basis of preliminary herbarium studies, both *f. microphyllum* and *f. genumum* appear to be also present in North America. A closely related species, *V. occidentale* Gray, is found in the mountains of western North America. Of further interest is the fact that large clones are known from the *V. uliginosum* population on Mt. Marcy, Adirondack Mountains, N. Y., which bear considerable resemblance to the western *V. occidentale*.

^j Reported here for the first time. The chromosome counts were made from plants raised from seed grown in the experimental greenhouses at the Plant Industry Station, Beltsville, Maryland.

stance, they have been found growing where both tetraploid and hexaploid plants were present. These pentaploids vary considerably in fruitfulness; some have almost no fruit; others have small crops of fruit which contain but few seed; and at least one clone has been found which fruits heavily but

is essentially seedless. In this instance the fruit is of rather large size, although lacking in flavor.

One plant which flowered freely in the test plots and bears fruit, was found to have a somatic set of 50 chromosomes ($4x + 2$). This is the first report of aneuploidy in the genus. Neither aneuploids nor pentaploids are likely to give rise to populations worthy of specific recognition, although there is a strong possibility that they may yet have considerable horticultural value.

So far, we have been unable to pay more than passing attention to meiotic phenomena and the physical aspect of individual chromosomes. The work of Hagerup (7, 8, 9) on a hexaploid form of *Orycoccus* (= *Vaccinium*) cannot be taken as an indication of the usual condition of hexaploids in *Vaccinium*. There is little question that the sterility of some few hexaploids known to us may be of the same type, and results from improper cleavage and ultimate break-down (abortion) of the microspores; certainly this is true in various pentaploids. But the high degree of fertility, together with the production of hybrid combinations and expected segregate forms, is sufficient proof that normal meiotic processes are involved in the vast majority of the hexaploids with which we have worked. Our investigations indicate that there is relatively no more abortive sterility among hexaploids than is to be found in tetraploids or diploids.

In the early years of the blueberry breeding work all material brought into the experimental plots from the wild was highly selected, particular attention being paid to its fruitfulness, or to some unusual character. Recently, it was suspected that, by selecting in this manner, individuals have been studied which, cytologically, were not representative of the natural populations. This has since proved to be the case in several instances and explains certain of the errors in earlier nomenclatural interpretations based on this material. Since 1938, more and more attention has been paid to the aspect of natural populations. In fact, many of the plants used in the present report have been random selections, care being taken only that they did not deviate from the norm of their particular group. Others have been chosen because they presented particular problems of interpretation. Briefly, then, attention to these items has permitted us to attack the various problems from a broader viewpoint and has given us greater confidence in our general conclusions.

By the very nature of the genus, a knowledge of the chromosome number of individual plants is a necessity in the horticultural development of the group. Our present care to see that many of the plants studied are also representative of natural populations is of considerable importance in the taxonomic interpretations of its species. And while we certainly do not hold that chromosome numbers ultimately determine the nomenclatural dispo-

sition of a set of plants, we do feel that such information is necessary for their correct placement in the phyletic scheme of a genus. This paper, then, is merely a presentation of one set of basic facts concerning individuals, more-or-less characteristic of certain wild populations of *Vaccinium* and its relatives. Additional facts are necessary for the delimitation of species and the application of a functional nomenclature. A discussion of these facts and the relations and phyletic development of the species will be taken up in later papers, as well as a summary of the factors to be considered in the development of new horticultural material.

SUMMARY

An annotated list of the various species of *Vaccinium* whose chromosome numbers are known is presented. Among these the following are listed here for the first time.

American species: The diploids ($2n = 24$) are: *V. angustifolium*, *caesariense*, *crassifolium*, *elliottii*, *darrowi*, *margarettae*, *ovatum*, *pallidum*, *parvifolium*, *tenellum*, *vacillans*, and a complex of hybrid origin and recognized in previous literature as *V. cuthbertii*. The tetraploids ($2n = 48$) are: *V. australe*, *brittonii*, *lamarekii*, *simulatum*, *tallapusac*, and *virgatum*. The hexaploids ($2n = 72$) are: *V. constablaei*, *amoenum*, and *ashei*. Pentaploid individuals ($2n = 60$) and a single aneuploid ($2n = 50$) ($= 4x + 2$) are also reported. Nomenclatural adjustments have been made in previous reports.

Asia Minor species: A single species from the Caucasus Mountains is reported here for the first time: *V. arctostaphylos* L., a tetraploid ($2n = 48$).

A list is also presented of all species of cranberry (*Oxycoccus*) recognized in a recently published study of the group. Recorded here for the first time are the chromosome numbers of two American species: *O. macrocarpus* (Ait.) Pers., a diploid ($2n = 24$). *O. ovalifolius* (Michx.) A. E. Porsild, a tetraploid ($2n = 48$). The "typical" material of *O. quadripetalus* Gilib. from Maine was found to be the same as that reported from European plants ($2n = 48$).

Several essentially circum-boreal species of *Vaccinium* whose chromosome complements are known only from the European material are listed, together with notes on possible correlations with the North American representatives of these same species.

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LEPTOSIRA MEDICIANA BORZI

W. N. STEIL

INTRODUCTION

Leptosira Mediciana was first found and described by Borzi (1883), who observed all of the stages in the life cycle except the germination of the zygote. Collins (1912) collected the alga in Massachusetts. It has not been found at any other time in this country.

Vischer (1933), fifty years after the discovery of *Leptosira Mediciana* by Borzi, found and described *Leptosira obovata*. In this species, he observed that the zoospores germinate directly.

The genus *Leptosira* belongs to the Trentopohliaceae, a family of the Chaetophorales, a comparatively large group of branched green algae the cells of which are uninucleated and possess single parietal chloroplasts.

In the latter part of February, 1937, the rare epiphytic alga, *Leptosira Mediciana*, was found growing on *Coleochaete scutata* Breb. This alga appeared in an aquarium into which, about three months earlier, there had been planted a small amount of *Nitella* collected in the vicinity of Milwaukee. There can be little doubt that the *Coleochaete* and the *Leptosira* were introduced into the aquarium with the *Nitella*.

About 80 per cent of the *Coleochaete* plants, which were not produced in large numbers, bore one or more *Leptosira* colonies. Since they were found only on the *Coleochaete* colonies and never on the sides of the aquarium, the alga, as has heretofore been reported, is undoubtedly epiphytic.

METHODS AND MATERIALS

By means of a hand lens, and sometimes with the naked eye, it was possible to observe the *Leptosira* on the *Coleochaete* colonies attached to the sides of the aquarium. The *Coleochaete* colony with the *Leptosira* was carefully removed and fixed for about twenty-four hours in a 25 per cent chromacetic solution, washed and dehydrated to 70 per cent alcohol. The plants were then stained in a modified Harris' haematoxylin solution for about two hours, washed with water, and gradually dehydrated to absolute ethyl alcohol. Some of the colonies were counterstained with a weak solution of fast green in absolute alcohol. After clearing with xylol, the colonies were run up to mounting balsam, by passing them through various grades of absolute xylol and balsam.

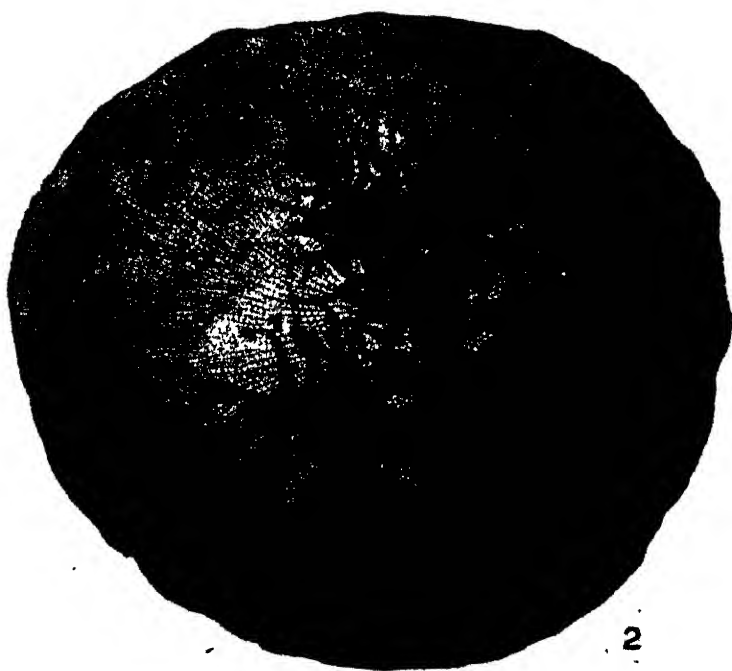
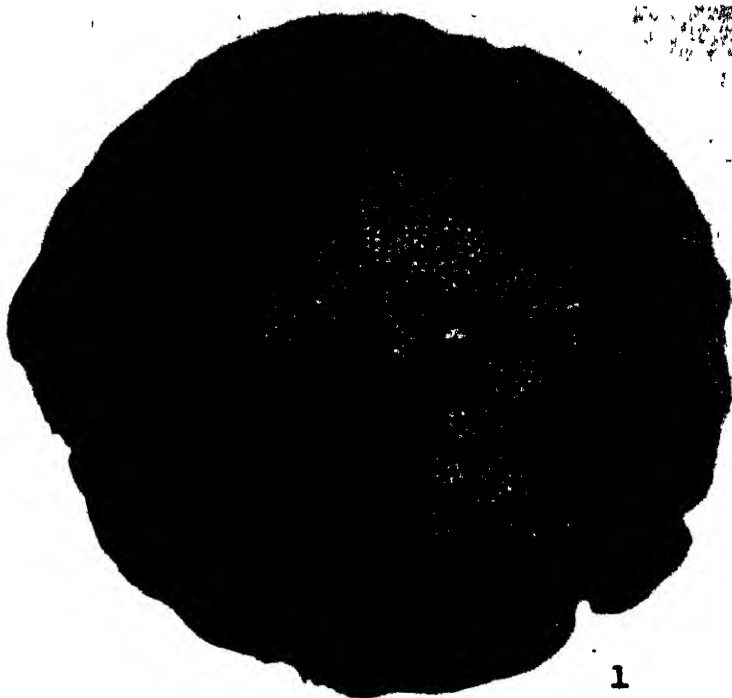


FIG. 1. A photomicrograph of the epiphytic *Leptosia Mediciana* Borzi colony borne by *Coleochaete scutata* Bieb. $\times 60$ approx. FIG. 2. A photomicrograph of several colonies of *L. Mediciana* Borzi borne by *C. scutata* Bieb. $\times 50$ approx.

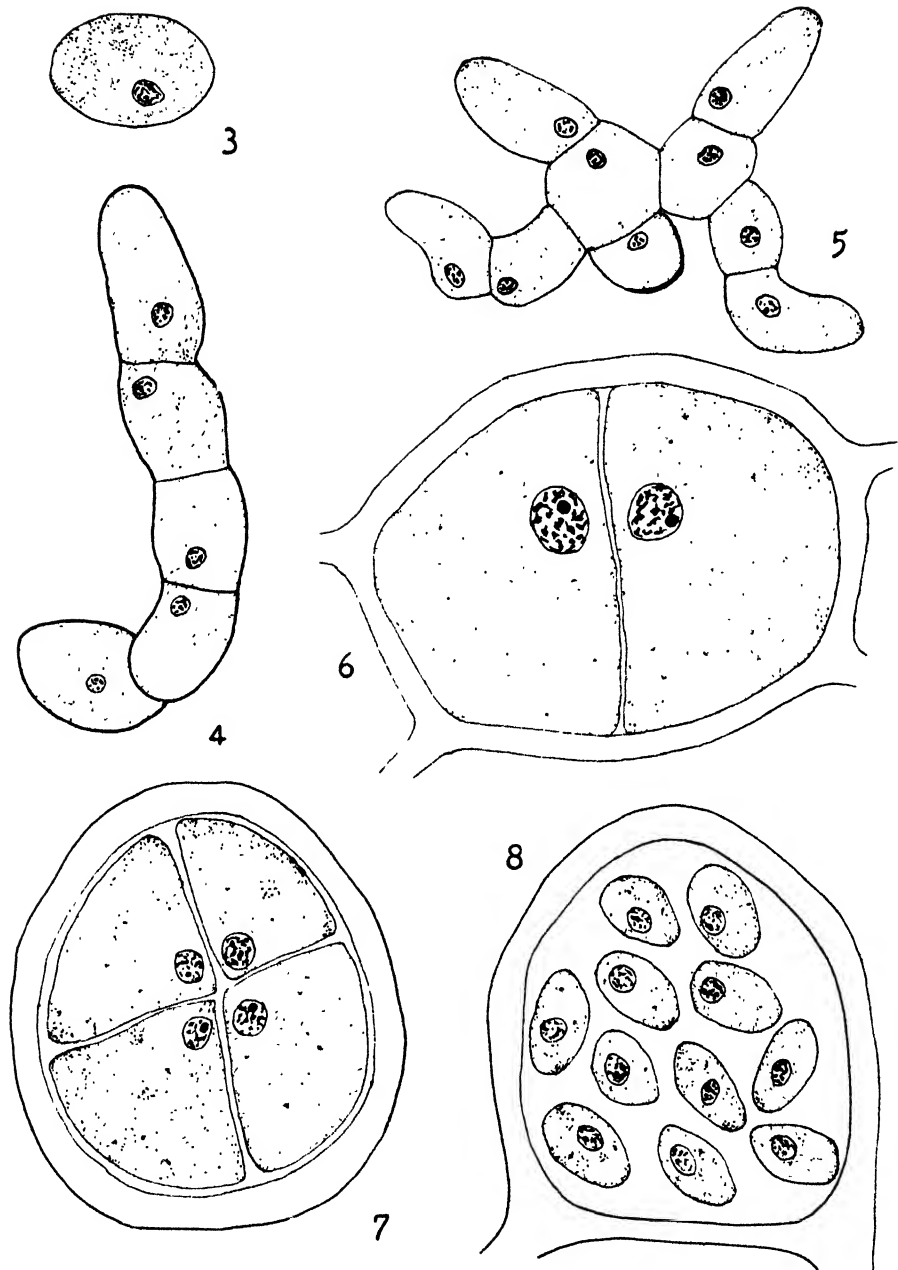


FIG. 3. A zoospore of *Leptosira Mediciana*. The flagella are not shown. $\times 1360$ approx. FIG. 4. A young filament produced by a germinating zoospore. $\times 1360$ approx. FIG. 5. A young branching colony. $\times 2800$ approx. FIG. 6. A two-celled stage of a zoosporangium. $\times 2800$ approx. FIG. 7. A four-celled stage of a zoosporangium. $\times 2800$ approx. FIG. 8. A zoosporangium showing some of the numerous zoospores. $\times 2800$ approx.

OBSERVATIONS AND DISCUSSION

Leptosira Mediciana, as has been described by Borzi, consists of radiating branched torulose filaments which taper gradually from base to apex. The larger and older cells of the colony are at its center (figs. 1, 2).

The cell of *Leptosira* is uninucleated and contains a single peripheral chloroplast of a yellow-green color. The plastid is without a pyrenoid. The cytoplasm is highly vacuolate (figs. 3, 4).

Most of the divisions of the cells of the colony are at right angles to the length of the filaments, although occasionally oblique divisions occur. Infrequently, the divisions are lengthwise in the cells.

There is a marked thickening of the walls of the *Leptosira* cells, beginning at the base of the filaments, or at the center of the colony (figs. 1, 2). As the thickening of the wall increases, the cells at the center of the colony form a mat or an incrustation.

The cells of which the walls become thickened function as zoosporangia. In the formation of the zoospores, the cell destined to function as a sporangium undergoes a division into two cells of approximately equal size (fig. 6). The next division results in four cells of nearly equal size (fig. 7). Many divisions of these cells then occur and numerous polygonal cells are formed, which round up and become zoospores which escape through a large pore in the wall of the sporangium (fig. 8).

No direct observations could be made on the germination of the zoospores since they were not produced in abundance. Whether they germinate directly or whether they form first *Characium*-like filaments, which produce four zoospores, as stated by Borzi (1883), could not be determined. However, some of the prepared slides showed such filaments which invariably contained four spores, each of which closely resembled in structure the *Leptosira* cell. That the zoospores may germinate directly, as has been described by Vischer in *L. obovata* is suggested by the numerous young colonies found occasionally in a nearly circular zone on the *Coleochaete* colony. One of these, an unbranched filament, is shown in figure 4. Another one of these, shown in figure 5 is a young branching colony. Earlier and later stages were readily found. Zoospores, one of which is shown in figure 3, were sometimes observed in the prepared slides to be abundant near empty zoosporangia from which they had undoubtedly escaped. Since no motile zoospores could be obtained, no attempts were made to stain the flagella of the zoospores.

Neither zoogametes, nor zygotes were at any time observed during the course of the investigation extending over a period of about six months.

SUMMARY

1. *Leptosira Mediciana* Borzi was found as an epiphyte on *Coleochaete scutata* Breb.

2. The radiating torulose filaments of the colony form a dense matted basal portion.
3. The cells of the colony divide most frequently at right angles to their length.
4. Any cell may function as a zoosporangium.
5. In the formation of zoospores, numerous successive divisions occur in the mother cell of the sporangium.
6. The zoospores, it is suggested, germinate directly.
7. Single celled *Characium*-like filaments are formed which produce four cells, probably spores.
8. Motile zoospores and zygotes were not observed in *Leptosira Mediciana* Borzi.

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COMPARATIVE STRUCTURE OF GREEN LEAVES OF ORIENTAL TOBACCO AT DIFFERENT LEVELS ON THE STALK IN RELATION TO THEIR QUALITY UPON CURING¹

FREDERICK A. WOLF AND E. FELTON JONES

The commercial tobaccos produced in different regions of the world differ greatly in quality.² These differences are commonly attributed to responses induced by differences in soils, climates, and cultural practices employed. The proximate causes of these variations in quality, however, are multiple and complex, and remain far from being completely understood. Even though this is the situation the quality of the final product in each region has become stabilized to a high degree in consequence of standardization of empirical practices involving cultivation, fertilization, harvesting, curing, storage during aging and fermentation, and other manipulative procedures.

In the case of flue-cured tobaccos, our previous studies (Darkis *et al.* 1936, Wolf and Gross 1937) have shown that quality is closely correlated with the level at which the leaf is borne on the stalk. Stalk position is in turn correlated with the chemical composition of the leaf, both as regards mineral and organic components. Furthermore, both chemical composition and leaf structure may be modified and hence may be controlled to an important degree by the cultural practices of topping (removal of the inflorescence) and stickering (removal of axillary buds that develop after decapitation). A body of additional unpublished data from our studies gives further support to these conclusions. Numerous studies involving causes of differences in quality of types of tobacco other than the flue-cured varieties, grown in this country or in other areas, are neither so extensive nor intensive, and the results are consequently less precise (Nelson 1928, Berthold 1929a, 1929b, Smirnov 1933, Avery 1934, de Montero 1938).

During the past four seasons oriental or Turkish types of tobacco have been grown at the Tobacco Experiment Stations at Chatham, Va., and

¹ Studies conducted in cooperation with the Department of Chemistry, Duke University. Acknowledgment is made of aid given by Drs. F. R. Darkis and P. M. Gross of that Department. The help of Miss Nancy Bentley and Miss Christina Changaris is also acknowledged with gratitude.

² The meaning of the term "quality," as applied to oriental tobaccos, cannot be defined adequately. It includes many features whose appraisal by tobaccoists has been gained largely from experience. Judgment of quality has been perfected by them to the extent that it may be regarded as an art. Tobaccoists, to judge quality, employ the senses of touch, sight, and smell, arranged in order of importance.

Oxford, N. C. In connection with this work it appeared advisable to give consideration to the problem of quality of the product by utilizing methods of study patterned after those that had been employed previously in studies of quality among flue-cured varieties of tobacco. The present report is concerned with the results obtained from such studies.

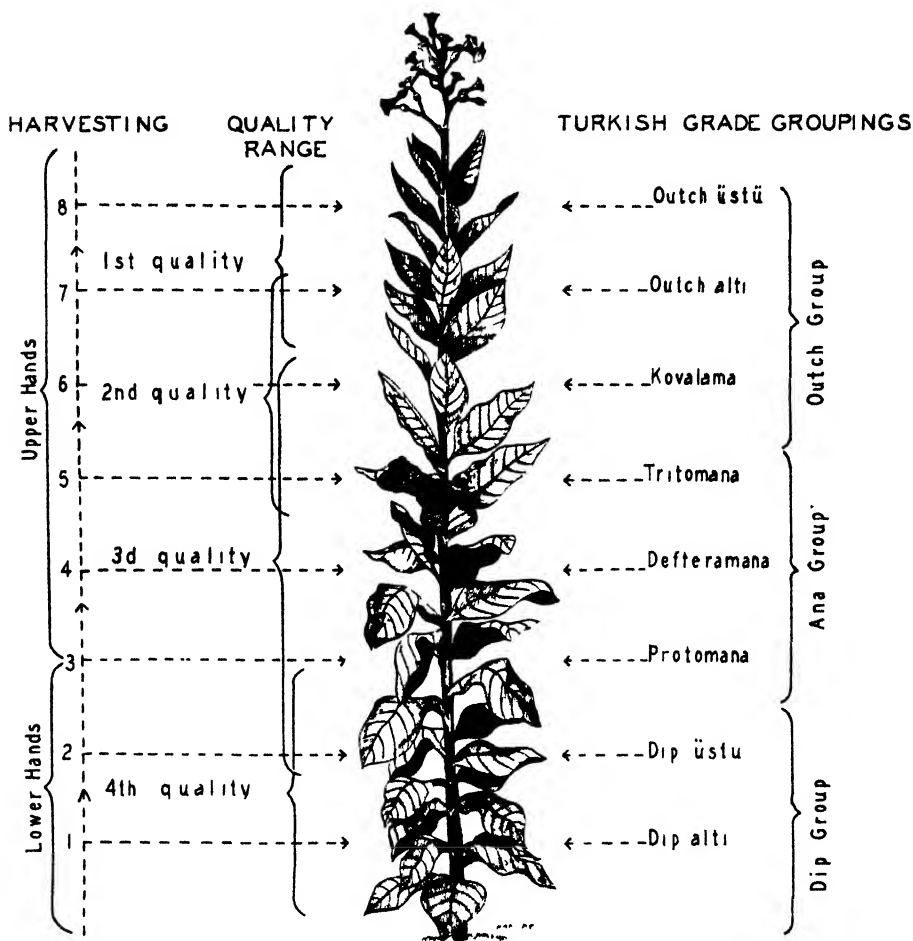


FIG. 1. Order of removal of leaves in harvesting Turkish tobacco, relation of stalk position to quality and to usage by the American tobacco industry, and probable grades as customarily employed in the Near East. Gradation on the basis of stalk position may not be adhered to strictly in actual practice, but nevertheless serves as a general guide.

There are numerous kinds of oriental tobacco, each characteristic of the region or district in which it is grown and marketed. Each differs from the others in quality, some to a very marked degree, as indicated by differences in shape, color, and texture of the leaf, and by differences in combustibility.

aroma, flavor, etc. These tobaccos have been grouped, however, into a small number of types, the most important of which are designated as Samsoun, Smyrna, Cavalla, and Xanthi.

In the cultivation of Turkish tobacco, from 50,000 to 70,000 plants per acre are grown, approximately ten times the number employed with flue-cured varieties. As a consequence of such close planting, the individual plants have slender stems, their leaves are small, and many varieties attain a stature of only about a meter. Leaves are harvested as they mature, beginning with the lowermost and progressing toward the top of the stalk, a process called "priming." Experience alone is the basis for judging when leaves are in prime condition. The quality of cured leaves may be sharply lowered if leaves are primed when they are either premature or over-ripe. Usually the removal of from 6 to 9 gatherings, called "hands," is required to complete the harvesting. The leaves are cured by air-drying. It is well known that stalk position is of primary importance in determining quality of the cured leaves; leaves of poorest quality are obtained from the first hand, and quality improves with each successive gathering thereafter (fig. 1).

MATERIALS AND METHODS

Five varieties of oriental tobacco, representing four important types, were used in the present studies: (1) Broussa of the Samsoun type from northern Turkey; (2) Ayassolouk, typical of Smyrna tobacco grown in western Turkey; (3) Stanimaka, representing the Cavalla type, from Bulgaria; and (4) Yenige and Djebel, of the Xanthi type, from northern Greece and Bulgaria. Cultivation of the latter kind is restricted to mountainous regions.

Seedlings were transplanted into the field during early May, and were spaced approximately 5 inches apart in rows which were 20 inches apart. Details regarding the soil, preparation of the field for planting, fertilization, cultivation, and rainfall—all important factors in the growth of oriental tobacco—are omitted for the reason that they are not regarded as pertinent to this report.

Three typical plants of each variety were selected for detailed analysis. As the leaves of these selected plants matured they were primed, and determinations were made of weight, area, thickness, and shape.

Leaf area, of both green and cured leaves, was determined by tracing the leaf upon a paper pattern which was weighed and compared with the weight of a paper standard of known area. Leaf thickness was measured by means of a Randall and Stickney gauge caliper provided with an 8 oz. weight and calibrated in units of 0.001 cm. Since a tobacco leaf is variable in thickness an average figure was obtained from a series of 6–10 measurements of each lamina (12–20 per leaf). These measurements were made

along a line extending from the leaf base to the tip, midway between the midrib and the margin. Leaf thickness was also determined by measurement of sections of leaf tissue prepared as follows: Samples of laminar tissue from leaves borne at a corresponding level on near-by plants were preserved in a formalin—acetic-acid—alcohol solution. These samples were dehydrated, embedded in paraffin, sectioned at a thickness of 25μ and stained with fast green. Crystals of the type known as druses are very abundant in leaves of oriental tobacco. These crystals, instead of being composed of calcium oxalate, as is commonly the case in seed plants, may be presumed,

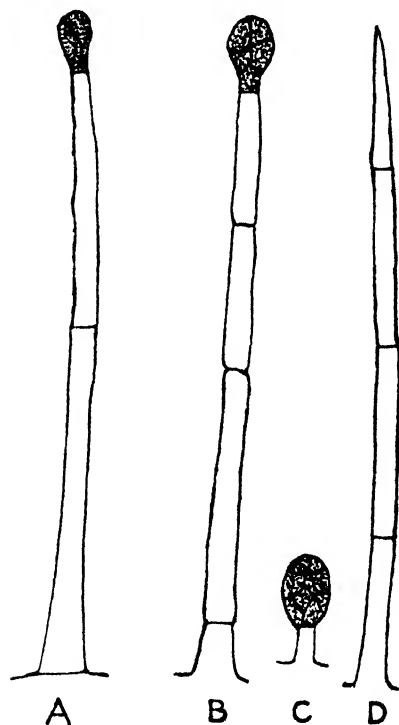


FIG. 2. Some types of trichomes from Turkish tobacco. Their length may exceed from two to three times the thickness of the intervinal parts of the leaf. A, hair with unicellular gland at tip; B, with multicellular gland; C, short-stalked hair with multicellular gland; D, non glandular hair.

from the work of Ridgway (1916), to be composed chiefly of calcium, potassium, and magnesium salts of citric and malic acids. The presence of these crystals interfered with the preparation of satisfactory sections. The difficulty of cutting suitable sections was in large measure obviated, however, by storing leaves in a moist chamber for 48 to 72 hours prior to fixation. Under these conditions the crystalline deposits largely disappear and make it easy to section embedded leaves.

The length and width of each leaf were determined from measurements of the paper patterns. Leaf length was regarded as the distance from leaf base to leaf tip, and leaf width as the distance across the broadest portion. In the figures as given for the length-width ratio, the width is considered as 1.00.

Hairs (trichomes; fig. 2) and stomata are present on both surfaces of tobacco leaves but whether each structure is equally as numerous on each surface remains unknown. Consideration was given in the present study to the number of hairs and stomata per unit area on the lower leaf surface. The materials examined consisted of portions of the lower epidermis stripped from the median region, using four leaves from each sampling. Examinations of epidermal strippings and counts for hairs were made with the low-power magnification of a microscope (100 \times). The figure presented for each determination is an average of four counts from each of the four leaves examined. An average measurement of maximum length and width of 16 stomata, as seen by high-power magnification (350 \times), was used in computing the volume of the stomatal apparatus. To calculate the volume of the stomatal apparatus, i.e., the pair of guard cells, it was regarded as an ellipsoid, and the formula: $\text{Volume} = \frac{\pi Dd^2}{8}$, in which D = length and d = diameter, was applied.

RESULTS

Since each Turkish tobacco plant produces from 25 to 40 leaves the data are too voluminous to be presented in their entirety. For this reason tabulations of averages have been assembled. In table 1, which relates to the dimensions, area, and weight of the leaves produced, and of their changes in size during curing, each figure represents an average of 75–120 measurements; and figures dealing with ratio of leaf length to leaf width, width being regarded as unity, represent twice as many measurements.

Each figure in table 2 represents 20–100 measurements, whereas each of those in table 3 represents approximately six times as many, and each figure in table 4 is derived from a minimum of 16 determinations.

As regards height of plants and size of leaves, the plants used in these studies compare favorably with the same varieties when grown in the Near East, as confirmed by observers familiar with oriental tobacco who have seen our plantings. Differences between varieties are apparent in table 1. Djebel, an early-flowering variety, has the smallest plants and its yield is lowest. Broussa, Ayassoulouk and Stanimaka, late-flowering varieties, yield most, and Yenige, which is intermediate in date of flowering, is also intermediate in yield.

That a definite leaf shape is characteristic of each variety is suggested by the length-width ratios. The leaves of Broussa are petiolate and lack

auricles, or at most have narrow ribbon-like auricles. Leaves of this type are termed "koulaksis" (earless). The leaves of Djebel, Ayassoulouk, and Stanimaka are sessile, having broad auricles, and are of the type called "kabakoulak" (broad-eared); those of Yenige, also sessile, are narrow and lancet-shaped, a type called "sirdilli" (ox-tongue-like).

During curing of the leaves shrinkage in length is proportionately less than shrinkage in width. This condition may be presumed to arise in consequence of the position of the "skeletal" tissues, i.e., the midrib and larger

TABLE 1. *Gross features of the leaves of five varieties of oriental tobacco.*

		Variety				
		Broussa (Samsoun)	Yenige (Xanthi)	Stanimaka (Cavalla)	Djebel (Xanthi)	Ayassoulouk (Smyrna)
Total leaf area per plant, cm ²	Green	4956	3573	4427	2592	4864
	Cured	3198	2328	2739	1726	3018
Average leaf dimensions, cm.	Green	19.4	21.2	18.4	15.9	21.0
		× 12.3	× 7.5	× 10.1	× 10.0	× 10.5
	Cured	16.9	19.7	15.3	13.6	17.7
		× 9.5	× 5.9	× 7.7	× 7.8	× 8.0
Average length width ratio of leaves	Green	1.57	2.82	1.83	1.59	2.00
	Cured	1.78	3.34	1.98	1.74	2.20
Total leaf weight per plant, gm.	Green	151.1	118.1	121.4	69.1	136.9
	Cured	22.2	14.5	16.8	9.8	20.8
Reduction of leaf area during curing to per cent of green leaf area	Average %	64.3	65.1	61.8	66.5	62.1
Number of leaves required for pound of cured tobacco	Average	610	943	808	1018	650

secondary veins. The loss in leaf area during curing ranges between 30 and 40 per cent, and there is no reason for believing that amount of reduction in size is characteristic of a given variety. This opinion is supported in part by other data assembled in tables 2 and 3.

Appreciation can be gained from data in table 2 of differences among oriental varieties in leaf size and shape at the different stalk positions, and of the changes in length-width ratios which occur during curing.

It is apparent from table 2 that the largest leaves occur near the base of the stalk and are those usually removed at the second or third priming. Proportion of leaf length to width varies with primings in some varieties

but does not do so in others. In the cases of Broussa and Yenige, except for the last priming, the leaves become proportionately longer in relation to their width as one progresses from the bottom toward the top of the stalk. Premature harvesting of the uppermost leaves occasioned by extremely dry weather may account for this exception. The leaves of Ayassolouk, on the other hand, tend to become wider in proportion to their length as the tip

TABLE 2. *Size and shape of oriental tobacco leaves of several varieties in relation to level on the stalk.*

			Priming						
			1st	2nd	3rd	4th	5th	6th	Average
Average leaf area, cm. ²	Broussa (Samsoun)	Green	167.3	261.9	254.6	187.2	120.9	53.3	174.2
		Cured	108.8	166.2	168.7	121.2	76.2	35.1	112.7
	Yenige (Xanthi)	Green	138.1	246.7	188.9	141.0	81.3	41.4	139.6
		Cured	88.6	165.1	122.7	88.4	55.2	26.3	91.1
	Stanimaka (Cavalla)	Green	177.0	293.1	266.7	186.1	85.1	39.1	179.5
		Cured	111.8	174.3	165.6	112.3	52.3	23.9	106.9
	Djebel (Xanthi)	Green	88.0	144.3	153.4	90.8			119.1
		Cured	54.7	92.5	95.9	62.7			76.4
	Ayassolouk (Smyrna)	Green	240.9	277.4	234.9	129.8	66.9	49.5	166.6
		Cured	149.7	187.6	149.9	79.0	42.6	31.9	99.5
Length width ratio of leaves	Broussa (Samsoun)	Green	1.41	1.51	1.55	1.66	1.74	1.61	1.58
		Cured	1.57	1.71	1.78	1.81	1.76	1.75	1.73
	Yenige (Xanthi)	Green	2.44	2.63	2.86	2.87	2.91	2.82	2.75
		Cured	3.05	2.98	3.09	3.19	3.20	3.11	3.10
	Stanimaka (Cavalla)	Green	1.79	1.80	1.83	1.88	1.80	1.78	1.81
		Cured	1.98	1.98	1.98	2.15	1.96	1.84	1.98
	Djebel (Xanthi)	Green	1.66	1.51	1.52	1.64			1.58
		Cured	1.80	1.84	1.75	1.67			1.76
	Ayassolouk (Smyrna)	Green	2.12	1.98	2.05	1.99	1.95	1.90	2.00
		Cured	2.33	2.22	2.21	2.16	1.95	1.93	2.14

of the stalk is approached. All the leaves of Stanimaka, however, tend to be alike in length-width ratio, regardless of their stalk position.

The data in table 3 deal with differences in leaf thickness, in per cent of dry substance, and in shrinkage, during curing, of successive primings.

In all varieties studied, the thickest leaves were in the first priming, and they progressively become thinner toward the top of the stalk. The figures representing thickness of sixth primings are in each case in error as shown by diagrammatic representations of cross sections of Broussa, Yenige, and Ayassolouk leaves (figs. 3, 4, 5). The error in measurements with the caliper

arose because the diameter of the circular disk of the calipers which comes in contact with the leaf is approximately 6.0 mm., a distance exceeding that between the veins of small leaves.

TABLE 3. *Thickness of green leaves, water loss, and shrinkage during curing of several varieties of oriental tobacco.*

		Priming					
		1st	2nd	3rd	4th	5th	6th
Average thickness of leaves, μ	Broussa (Samsoun)	305	290	278	254	249	262
	Yenige (Xanthi)	297	295	257	247	226	256
	Stanimakka (Cavalla)	325	272	235	243	218	249
	Djebel (Xanthi)	328	302	286	241		
	Ayassolouk (Smyrna)	273	260	234	225	234	238
Reduction of leaf area during curing to per cent of green leaf area	Broussa (Samsoun)	64.6	63.5	66.2	64.7	63.0	65.8
	Yenige (Xanthi)	64.2	66.9	65.0	62.7	67.9	63.5
	Stanimakka (Cavalla)	63.2	59.5	62.1	60.3	61.5	61.1
	Djebel (Xanthi)	62.2	64.1	66.2	69.0		
	Ayassolouk (Smyrna)	62.1	67.6	63.8	60.9	63.7	64.4
Average dry weight of cured leaf as per cent of green leaf weight	Broussa (Samsoun)	14.1	12.2	14.0	15.5	17.6	19.0
	Yenige (Xanthi)	11.1	10.3	13.7	15.0	15.3	15.3
	Stanimakka (Cavalla)	11.7	11.8	14.6	15.7	17.5	18.5
	Djebel (Xanthi)	12.9	12.9	13.7	18.1		
	Ayassolouk (Smyrna)	12.0	12.9	16.6	17.9	19.6	19.8

It is a common impression gained largely through the sense of touch that the upper leaves are thickest. This erroneous impression arises from (a) the large proportion of veins to interveinal tissue in small leaves, with conse-

quent greater rigidity; (b) the compactness of mesophyll cells, a feature that favors rigidity; (c) the much denser population of hairs that offers greater resistance to compression; and (d) the somewhat thicker cuticle of

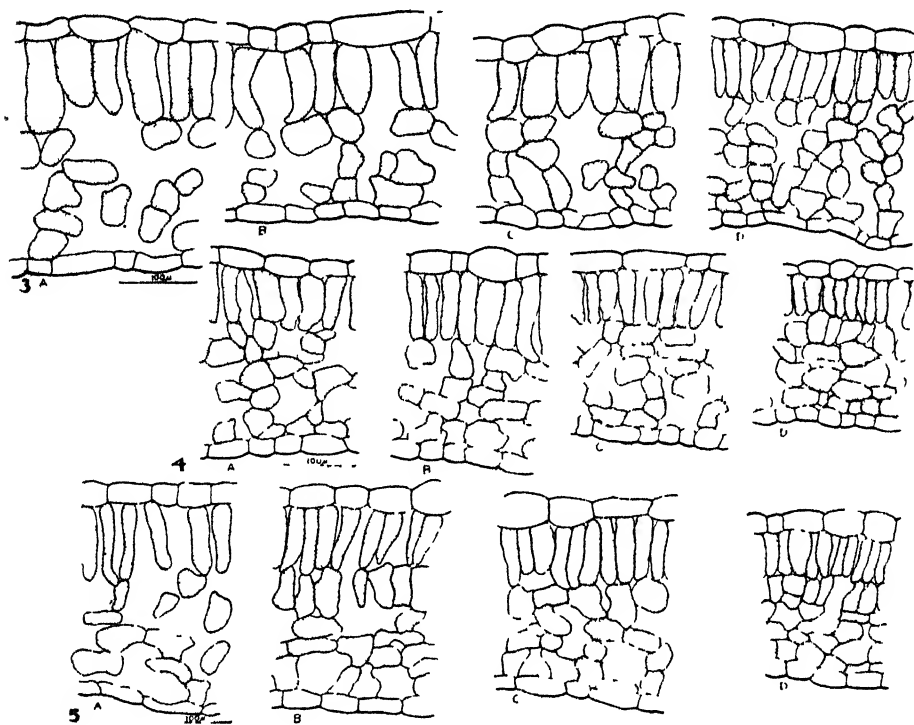


FIG. 3 (upper row). Semi-diagrammatic sketches, drawn to the same scale, of cross sections of leaves of *Broussa* tobacco, showing leaf thickness, constituent cell size, and arrangement of cells. A, from first priming; B, from third priming; C, from fifth priming; D, from seventh priming. The upper horizontally arranged cells are upper epidermis, the subjacent vertically arranged cells are palisade parenchyma, the loosely arranged, irregular cells beneath the palisade parenchyma are spongy parenchyma, and the lower, horizontally arranged cells are lower epidermis. The trichomes or hairs produced by both the upper and lower epidermis are not shown. FIG. 4 (middle row). Cross sections of leaves of *Yemge* tobacco, drawn to scale, representing semi-diagrammatically leaf thickness, cell size, and cell arrangement of leaves of different primings; A, from leaves of the first hand; B, from the third hand; C, from the fifth hand; and D, from the seventh hand. The median tissues are palisade parenchyma above, and spongy parenchyma below. Leaf hairs are not shown. FIG. 5 (lower row). Semi-diagrammatic representations, drawn to scale, of cross sections of *Ayassolouk* tobacco leaves. Relative leaf thickness and constituent cell size and cell arrangement from leaves of different primings are shown; A, taken from the first hand, B, from the third; C, from the fifth; and D, from the seventh. None of the trichomes is shown.

the uppermost leaves. Dry weight increases with increased level of the leaf on the stalk, and is approximately 50 per cent greater in the uppermost leaves than in those of the first priming.

The data do not indicate significant differences in shrinkage of leaves at different stalk positions.

The population of glandular hairs and that of stomata per unit area of leaf, on the lower leaf surface, at four levels of insertion, are shown in table 4.

It is apparent that there are many more glandular hairs per unit area of leaf on the smallest leaves than on the largest ones, the calculations indicating 2-5 times as many. Moreover there are 50-100 per cent more stomata

TABLE 4. *Comparison of varieties of oriental tobacco as to population of glandular hairs and stomata on the lower leaf surface.*

Variety	Stalk region	Number of hairs per cm. ²	Approximate number of hairs per entire lower leaf surface	Number of stomata per cm. ²	Volume of stomatal apparatus, μ^3
Broussa (Samsoun)	Lower	1577	263,832		22,209
	Lower median	1106	289,561	1269	27,635
	Upper median	1739	325,541	1447	21,800
	Upper	3571	311,034	1757	16,070
Yenige (Xanthi)	Lower	877	121,113		29,289
	Lower median	729	138,510	1187	37,016
	Upper median	1269	140,859	1692	26,416
	Upper	3661	151,545	1724	20,116
Stanimaka (Cavalla)	Lower	810	148,680		25,652
	Lower median	641	144,856	970	28,021
	Upper median	1665	141,691	1757	25,128
	Upper	2976	148,800	1709	17,899
Djebel (Xanthi)	Lower	787	125,920		23,836
	Lower median	740	130,720	943	32,242
	Upper median	1070	138,463	1546	38,314
	Upper	1533	141,012	1773	23,620

on unit areas of small leaves than on those of large ones. Unfortunately total area of each leaf from which the strippings were made was not measured. Approximations of the number of hairs on the lower side of the leaves for the four indicated regions were therefore calculated on the basis of leaf sizes as represented in table 2. On this basis, interpretation of the calculated numbers of hairs per leaf would indicate, for a given variety, that each leaf tends to have the same hair population.

The average volume of the stomatal apparatus of large leaves is in turn greater than that of small leaves. Presumably differences between leaves in volume of stomatal apparatus are of the same magnitude as those of the other leaf cells and this factor is therefore correlated with leaf size.

INTERPRETATIVE DISCUSSION

Upon attempting to elucidate the proximate causes of differences in

quality of Turkish tobaccos, the evidence indicates that these causes center around certain interrelated and mutually interdependent factors, as follows:

- (1) Leaf size is correlated with stalk position;
- (2) Leaf size is correlated with cell size;
- (3) Differences in quality are correlated with differences in metabolic activity of leaves borne at different stalk positions;
- (4) Increase in population density of glandular hairs and other trichomes per unit area of lower leaf surface is correlated with increase in quality of tobaccos.

Each of these factors, in turn, will be given separate consideration, although each one is intimately related to and has bearing on each of the others. For this reason it is essential that this entire discussion be considered as a unit so as to avoid isolating ideas from their context.

1. Leaf Size and Stalk Position. As shown by data in table 2, the largest leaves produced in oriental tobaccos occur along the basal portion of the stalk. It is well known among tobaccoists that quality of Turkish types is correlated with the level at which the leaves are borne on the stalks and that high quality is seldom if ever to be found in lowermost leaves but rather in the smallest uppermost ones. Furthermore, there are reasons for believing that no matter how small the lowermost leaves, they can never be made to possess high quality. Such leaves, regardless of care during curing, are not acceptable for export and have almost never been utilized by the American tobacco industry.

The application of excessive amounts of fertilizer, or the wide spacing of plants may cause all the leaves of a plant to be larger than is normal for a given variety. As a consequence all leaves on such plants are lowered in quality. This conclusion is supported not only by results obtained in our own production of Turkish tobaccos but also by the experiences of many persons well informed on tobacco culture in the Near East. An understanding of the underlying causes of this decline in quality with increase in leaf size must take into account the fact that, in the Near East, tobacco has been cultivated for years in soils of low natural fertility and in areas having protracted periods without appreciable rainfall. Under such influences the plants are dwarfed. Then, as an additive cause for dwarfing, account must be taken of the fact that competition for water, nutrients, and light has been intensified by the cultural practice of close-spacing in the field. Under these conditions it should be anticipated that the tobacco plants would be depauperate and would differ structurally and physiologically from plants grown under conditions which would permit vigorous development.

2. Leaf Size and Cell Size. Avery (1933), studying the development of leaves of *Havana*, *Cuban Shade*, and *Cash* varieties of tobacco, found that

when the leaves attained approximately from one-sixth to one-fifth of their mature size their full complement of parenchyma cells had already been formed. Subsequent growth of leaves was due, therefore, not to the production of new cells but to enlargement of cells already formed. It may be implied from these observations that all mature tobacco leaves of a given variety, regardless of size, presumably contain approximately the same number of cells. This proved to be true with flue-cured tobacco leaves in which a study was made of structural changes induced by topping and suckering practices (Wolf and Gross 1937).

From examination of cross sections of leaves of Turkish tobacco from different stalk positions (figs. 3, 4, 5), it may be concluded that in Turkish tobacco also each leaf of a given variety has approximately the same number of cells. The volume of intercellular spaces is proportionately greater in large leaves than in smaller ones, but even if this fact be disregarded, there appears to be direct correlation between leaf size and constituent cell size. Attempts to establish such correlation by measurements of mesophyll cells were not made because of difficulties inherent in measuring cells so irregular in shape. The volume of the stomatal cells of leaves of different sizes, however (table 4) indicates the existence of correlation between leaf size and size of stomatal cells, and it is a reasonable assumption therefore that leaf size and size of other constituent cells is also correlated.

If the problem of securing quality like that in oriental tobacco types involved simply the production of plants having small leaves, composed of small cells, it should be possible to grow tobacco having such quality by use of seed from other genetic types, provided the same practices of cultivating, harvesting, and curing were followed. Our limited attempts to accomplish this by use of flue-cured types have not realized this goal. In extenuation, it must be remembered that the development of quality characteristic of Turkish types has been accomplished in response both to environmental factors acting over a period of 200 or more years, and indubitably also to hereditary factors.

From our limited observations it may be pointed out, as having bearing on the influence of heredity, that plants having upper leaves larger than average may be secured by judicious seed-plant selection. Moreover the quality of upper leaves from progeny thus selected is indicated to be high. Further evidence of the relation of hereditary factors to quality that appears to have more fundamental significance than results of selection for increased leaf size is the fact that the tobaccos produced have improved in each successive crop over the four-year period of these experiments. Instead, according to common opinion, a gradual deterioration of quality should have been expected.

3. Metabolic Activity of Leaves at Different Stalk Positions. Proof of differences in metabolic activity between leaves produced at different stalk positions rests upon a body of evidence, both direct and indirect, as follows:

(a) The dry substance content of leaves, as calculated on a green weight basis (table 3), increases progressively upward on the stalk, and may be at least 50 per cent greater in the uppermost leaves than in the basal ones. Undoubtedly a portion of this increase in the upper leaves may be accounted for by their greater proportion of cell wall substance (cellulose and cellulose-like materials), as may be inferred from examination of figures 3, 4, and 5. There should also be relatively more protoplasmic material and less vacuolar material in small cells than in large ones. From chemical analyses, to be presented in another report, it can be shown that significant differences exist in carbohydrates, proteins, and minerals between leaves borne at different levels.

(b) Leaves from different stalk positions, as shown by the varieties Broussa, Yenige, and Ayassolouk (table 3), differ in shape. The fact that they progressively tend to become relatively longer and narrower, or else shorter and wider, upwards on the stalk, is not believed to be fortuitous. Instead it is related to physiological unbalance in axial and abaxial forces, perhaps hormonal in nature, that control leaf shape. That such is the case was postulated to explain differences in length-width ratio of flue-cured tobacco leaves in response to topping and suckering practices (Wolf and Gross 1937). This unbalance with Turkish types of tobacco, which normally do not require topping and suckering, can be interpreted, however, as a response to priming only. With the removal of hand after hand, there remains a smaller and smaller functional leaf area, whereas the root and stalk systems remain intact.

It was pointed out long ago by Zalenski (1904) in studies on structure of tobacco leaves that the higher the leaf position on the stalk the smaller the size of constituent cells, the smaller their stomata, the thicker their cuticle and the stronger their relative development of mechanical tissues. He found that these upper leaves have a higher rate of assimilation and transpiration and interpreted the anatomical features therefore to indicate xeromorphism. This explanation completely ignores responses that seem traceable rather to physiological unbalance.

That priming, per se, can induce responses does not appear previously to have been taken into consideration by anyone. Data on length-width ratio of leaves from our previous studies (Wolf and Gross 1937) if regrouped, show that priming has a real influence which was indeed overlooked. This can best be shown by the rearrangement of our previous data shown in table 5.

The leaves of low-topped plants are seen to become progressively wider toward the top of the plant, those of the non-topped ones progressively

TABLE 5. *Response of flue-cured tobacco to topping and suckering; from tables 1, 2, 3, Wolf and Gross 1937, grouped by primings.*

Priming	Length-width ratio		
	Low-topping	High-topping	Non-topping
1st	1.802	1.871	1.845
2nd	1.785	1.797	1.905
3rd	1.769	1.910	1.947
4th	1.754	1.950	1.994
5th	1.608	1.954	2.195

longer, and the length-width ratio of high-topped ones is least modified. To account for the changes in leaf shape in non-topped plants priming appears to constitute the sole causal factor, and these resultant changes must be regarded as compensatory. The physiological unbalance from priming, indicated by changes in leaf shape, however, is not the same in all Turkish types, as shown in table 3. With some varieties the axial forces operating in determination of leaf shape may become progressively more and more dominant as harvesting proceeds; with other varieties both axial and abaxial forces may tend to remain balanced, or with other ones the abaxial forces may gain the ascendancy.

Profound compensatory responses, then, occur in tobacco plants that are "maimed" either by topping, suckering, or priming, and are to be compared with those induced among other kinds of plants. For example, fruit growers, gardeners, and florists have long employed such practices as thinning of fruit, removal of flower buds and branch buds, root-pruning, withholding of nutrients and water, judicious spacing of plants, leaf-pruning, etc., to modify the size and quality of the products grown for harvesting. Such responses prove the well-known fact, sometimes overlooked and unappreciated in experimentation, that the entire plant is a unit, behaving as a coordinated interdependent entity, and that the removal of any part induces responses in the "maimed" remainder. Such responses are fundamentally analogous to Le Chatelier's physico-chemical principle which states in effect that if some stress, as for example change in temperature, pressure, or concentration is brought to bear on a system in equilibrium and the equilibrium is thereby displaced, a change in the system occurs in that direction which tends to minimize the effect of the stress. A similar basic principle, as applied to living things, has been concisely brought into perspective by Cannon (1929) and is designated by him as homeostasis. Included in homeostasis are all those coordinated physiological reactions which function to maintain the steady states or equilibria in living organisms.

(c) The rate of growth of the upper leaves of tobacco is slower than that of the lower ones. This fact was pointed out by Berthold (1929a), and

is a matter of common knowledge among tobacco growers. Decrease in growth rate or decrease in metabolic activity is no doubt causally related to the age of the plant as a unit. The prevalence of supra-optimal temperature and light might serve as an additive cause of retardation of growth toward the end of summer. In any event, if Turkish tobacco grows intermittently and matures quickly the crop tends to be of poor quality, whereas if growth and maturity proceed uniformly and slowly, according to a typical growth pattern, the tobaccos will be of better quality.

4. Glandular Hairs and Quality. The hands and clothing of workers who harvest tobacco become covered with "gum." This gum consists of the exudate from glandular hairs that coat the leaves, stem, and inflorescence, admixed with fragments of the hairs themselves. Glandular hairs and other trichomes arise singly from epidermal cells, as is well known. Avery (1933) pointed out that the formation of new epidermal cells ceases shortly in advance of cessation of production of new mesophyll-tissue cells. Each leaf from a single individual plant appears, from the present observations (table 4), to possess substantially the same number of hairs. That each such leaf has the same hair population could be established with finality, however, only by determining at what stage of leaf development the production of new hairs ceases. Apparently such studies have never been made.

As is strikingly shown in table 4, the number of hairs per unit area of lower leaf surface is inversely proportional to leaf size. These results may be interpreted as showing that the amount of exudate is also inversely proportional to leaf size. Moreover, the warm weather that obtains as the season advances seems to stimulate increased activity of the glandular hairs so that droplets of exudate accumulate along the sides of the hairs and may even appear as pools or films around their bases.

The chemical nature of this exudate from the glandular hairs of tobacco leaves has been studied by several investigators but as yet our knowledge of it is quite incomplete. According to a recent summary by Brüchner, (1936) investigators seem in accord that the exudate is a mixture of resins or waxes and ethereal oils. These waxes, like the ethereal oils, are constituted of a mixture of aliphatic, hydro-aromatic and aromatic materials. Quite a few of the components have been isolated and their elementary composition and physical properties have been determined. During growth of a tobacco plant, and also during curing and fermentation, this exudate changes continuously by antiooxidation and polymerization.

Tobacconists generally are of the opinion that both flavor and odor of smoking tobaccos are directly correlated with the content of resins of the tobacco. This matter is summarized in the treatise of Brüchner (1936, vide p. 246) as follows: "Auf Grund der vorliegenden Untersuchungen kommen wir zu dem Ergebnis das der Qualität des Tabaks, die bekanntlich nur aus

dem Zusammenwirken aller Tabakinhaltskörper restlos erklärbar ist, im allgemein in einen direkten Verhältnis zu seinem Harzgehalt steht."³

Aroma in tobaccos has long been regarded as an elusive quality. In the case of Turkish tobaccos, the evidence outlined above may be interpreted to indicate that the characteristic aromas arise mainly from the glandular exudate. This interpretation rests mainly upon the observations that with progressive decrease in size of leaves there is a corresponding increase both in density of glandular hair population and in volume of aroma. Additional support for this explanation is offered by the observation that the glandular exudate, when isolated from leaves by accumulation on clothing, imparts to the clothing an aroma of great intensity characteristic of Turkish tobaccos. This aroma persists for a long time if the clothing is stored and even seems to change during storage.

SUMMARY

This study represents an attempt to correlate leaf structure and quality of oriental types of tobacco. It is concerned with five varieties, representative of four of the most important types, namely Samsoun, Smyrna, Cavalla, and Xanthi, that were grown at the Tobacco Experiment Stations, Oxford, N. C., and Chatham, Va., during four successive seasons.

The following correlations between the structure of green leaves and quality of cured leaves appear to be established:

1. Leaf size is correlated with stalk position, the largest leaves occurring at the basal portion of the stalk.
2. Leaf size is correlated with constituent cell size. Largest leaves have the largest most loosely arranged cells.
3. Leaves borne at different stalk positions may be of different shapes. Variations in leaf shape, interpreted as a compensatory response to priming, are greater and greater as harvesting proceeds. Differences in stalk position of leaves is also correlated with differences in amount of leaf-tissue constituents.

4. The population density of glandular hairs increases with decrease in size of leaves. The smallest leaves on a plant may have from 2 to 5 times as many hairs per unit area of leaf surface as the largest ones.

Since the largest leaves occur at the basal portion of the stalk and since the quality of the tobaccos increases progressively upward on the stalk, there is therefore direct correlation between structure and quality.

The proximate causes of differences in quality of oriental tobaccos are complex. Combustibility and aroma are well known to constitute the two

³ Freely translated: "On the basis of the foregoing experiments we may conclude that quality in tobacco although it can only be finally explained on the basis of the interaction of all constituents, yet it stands, in general, in direct relation to resin content."

most highly prized attributes of such tobaccos. Combustibility, not given consideration herein by direct tests, seems to depend mainly upon leaf texture, i.e., constituent cell size, and chemical composition. Aroma, when approached as a problem in leaf structure, seems to be traceable primarily to the exudate from glandular hairs.

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CHROMOSOME NUMBER, MEGASPOROGENESIS, AND DEVELOPMENT OF EMBRYO-SAC OF CLINTONIA

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The genus *Clintonia* contains six species, four of which are found in the temperate regions of North America. *Clintonia borealis* (Ait.) Raf. is the most widespread in its distribution, being found in moist woods from Labrador to North Carolina and westward to Manitoba, Minnesota, and Wisconsin. *C. umbellulata* (Michx.) Morong extends from New York to Tennessee and Georgia. Of the other two species, *C. uniflora* (Schult.) Kunth. is found growing in coniferous forests of the Sierra Nevada mountains and in scattered areas north to British Columbia, and *C. andrewsiana* Torr. is confined to shady woods near the coast in central and northern California.

The embryo-sac development of *Clintonia borealis* has been reported by R. W. Smith (4). He found that a single archesporial cell without division functions as the megaspore mother-cell. As a result of meiosis, four megaspore nuclei are formed. Three of these migrate to the chalazal end of the embryo-sac and degenerate, the fourth remains in the micropylar region, divides, and its daughter nuclei divide. Of the four nuclei thus formed, the two upper sister nuclei become the nuclei of the synergids. The nucleus nearest the chalazal end becomes the primary endosperm nucleus and the remaining one is the nucleus of the egg. In this study Smith reported also that the haploid chromosome number is probably 12.

Since this paper was prepared F. H. Smith (3) has observed that the embryo-sac of *C. uniflora* follows the same pattern of development as that described for *C. borealis*. He reports that the haploid number of chromosomes of *C. uniflora* is 14. Schnarf (2) in a summary of various types of embryo-sac development in angiosperms considered *Clintonia* a doubtful *Oenothera*-type, since the course of development does not agree with that of closely related plants. Maheshwari (1) has suggested that *Clintonia* may supply an example of a reduced embryo-sac of the *Fritillaria*-type with six instead of the normal eight nuclei. This is based only on a different interpretation of R. W. Smith's figures. A reinvestigation of *Clintonia borealis* was made by the present author, and the history of the development of the embryo-sac resembles that reported by Smith (4). A similar history was found in *C. umbellulata*, *C. andrewsiana*, and *C. uniflora*.

MATERIALS AND METHODS

Flower-buds of various ages and open flowers of *C. borealis* were collected by the author from the woods in the vicinity of Oosburg, Wisconsin. Similar material of *C. umbellulata* was obtained from J. Worden, St. Bonaventure College, St. Bonaventure, New York, and of *C. andrewsiana* and *C. uniflora* from Marion S. Cave, University of California at Berkeley, California. To them the author expresses her gratitude.

Material was fixed and imbedded in paraffin by the usual methods. Fixing fluids used were Carnoy's acetic-alcohol-chloroform, Randolph's CRAF, and formol-acetic-alcohol. The last-named fixative was used alone and also after first dipping the material in the Carnoy fixative. Sections were stained with Heidenhain's iron-alum haematoxylin. Chromosome counts were made in microspore mother cells in smears made with Belling's iron aceto-carmin. The Works Progress Administration, University Natural Science Project, Work Project No. 10324, furnished assistance in the preparation of some of the microscopic preparations.

CHROMOSOME NUMBER

Chromosome counts were made from polar views of heterotypic equatorial plates of micro- and megaspore mother-cells and of late prophase in the divisions of the micro- and megaspores. These counts are:

C. borealis: $n = 16$ (figs. 1, 2).

C. umbellulata: $n = 14$ (figs. 3, 4).

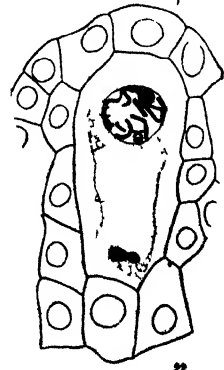
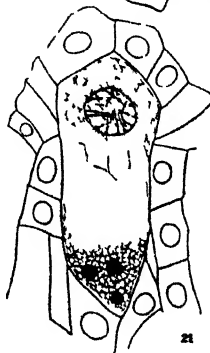
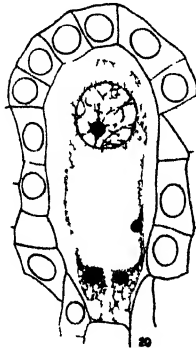
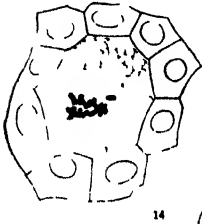
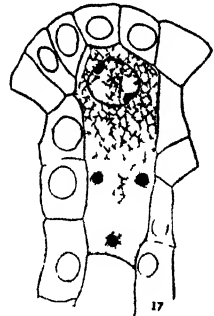
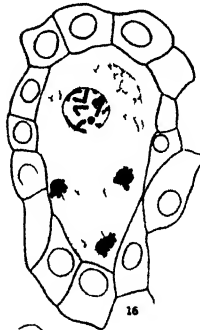
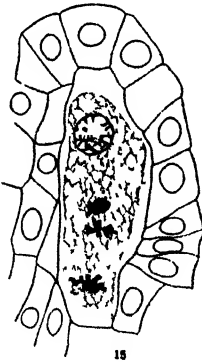
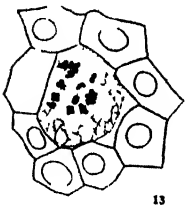
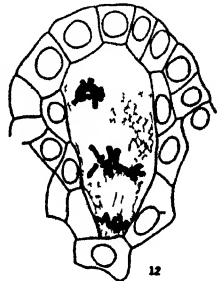
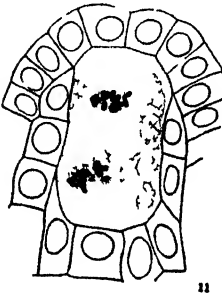
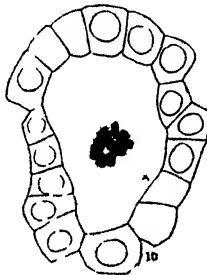
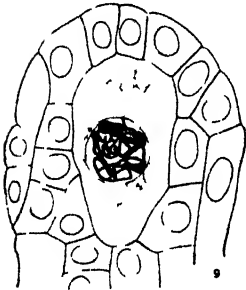
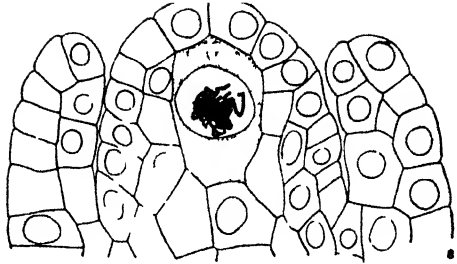
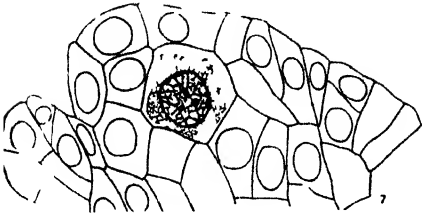
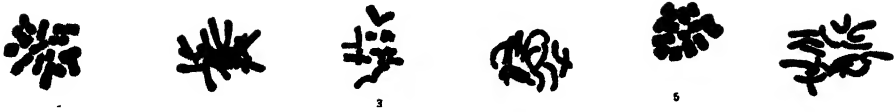
C. andrewsiana: $n = 14$ (fig. 5).

C. uniflora: $n = 14$ (fig. 6).

Explanation of figures 1-22

All drawings were made with a camera lucida at table level. Spencer compensating oculars and a 1.5 mm. 1.25 N.A. achromatic oil immersion objective were used. Figures 1-6 \times ca. 2000; 7-37 \times ca. 1200.

FIG. 1. Polar view of a heterotypic equatorial plate in the microspore mother cell of *C. borealis*. FIG. 2. Lateral view of a haploid equatorial plate of the final division in the embryo-sac of *C. borealis*. FIG. 3. Polar view of haploid equatorial plate in the second division in the embryo-sac of *C. umbellulata*. FIG. 4. Late prophase of first nuclear division in the microspore of *C. umbellulata*. FIG. 5. Polar view of heterotypic equatorial plate in the microspore mother-cell of *C. andrewsiana*. FIG. 6. Polar view of haploid equatorial plate of the final division in the embryo sac of *C. uniflora*. FIG. 7. Longitudinal section of young ovule with archesporial cell (megaspore mother cell) of *C. andrewsiana*. FIG. 8. The same in *C. umbellulata*. FIG. 9. The same in *C. uniflora*. FIG. 10. Lateral view, heterotypic equatorial plates in megaspore mother-cell, *C. umbellulata*. FIG. 11. Lateral view, homoeotypic equatorial plates in megaspore mother cell, *C. andrewsiana*. FIG. 12. Lateral view, anaphase, homoeotypic division in megaspore mother cell, *C. umbellulata*. FIGS. 13, 14. Equatorial plates, homoeotypic division in megaspore mother-cell, *C. uniflora*. FIG. 15. Four-nucleate embryo sac after homoeotypic division in *C. andrewsiana*. FIG. 16. The same in *C. umbellulata*. FIG. 17. The same in *C. uniflora*. FIG. 18. Migration of abortive nuclei in *C. umbellulata*. FIG. 19. After the migration of the abortive nuclei. FIG. 20. Embryo-sac of *C. umbellulata* with large central vacuole. FIG. 21. The same in *C. andrewsiana*. FIG. 22. Fusion of abortive nuclei in chalazal region of embryo-sac of *C. umbellulata*.



EMBRYO-SAC DEVELOPMENT

The history of the development of the embryo-sac in *C. umbellulata*, *C. andrewsiana*, and *C. uniflora* is in general similar to that described by R. W. Smith (4) for *C. borealis*, and by F. H. Smith (3) for *C. uniflora*. A single hypodermal cell is differentiated early in the development of the ovules as an archesporial cell which is to function as the megaspore mother-cell. It is easily distinguished from the neighboring nucellar cells by its greater size and its more deeply staining properties (figs. 7, 8). This cell increases in size slowly throughout the development of the embryo-sac. During the prophases of the first meiotic division it is about twice as long as broad, the nucleus being in the mid-region of the cell (fig. 9). The spindle of the first meiotic division lies near the center of the cell and approximately parallel to the long axis of the cell. Figure 10 shows this division in *C. umbellulata*; fourteen pairs of chromosomes can be counted on the equatorial plate.

The second meiotic division must follow almost immediately, since binucleate stages were rarely visible in the preparations. Only three prophase stages of second division were observed in my material. R. W. Smith (4) figured a binucleate cell in *C. borealis*, although he too reports that these are rare. The upper of the two nuclei is normal in appearance in his figure while the lower nucleus is an irregular mass of chromatin.

The axes of the homeotypic spindles may be approximately parallel to the long axis of the cell (figs. 11, 12) or at an oblique angle to each other (figs. 13, 14). Both divisions appear normal and occur simultaneously (figs. 11, 12). One exception was observed in *C. umbellulata*, in which the lower nucleus divided before the upper nucleus.

After reaching the poles (fig. 12), the chromosomes nearest the micropylar end of the developing embryo-sac become organized into a large rounded nucleus while the three other chromosome groups form irregularly shaped deeply staining masses (figs. 15, 16). Later these masses become rounded and often vacuolate but do not increase in size as does the micropylar nucleus (fig. 17). Spindle fibers persist for a time between the daughter chromosome masses, but eventually disappear. The cytoplasm is finely vacuolated and at no time is there any indication of a cell plate between the sister nuclei.

The embryo-sac grows, becoming several times as long as broad. The vacuoles, which up to this time have been small, now begin to coalesce, forming a large central vacuole in the center of the sac. This appears to occur earlier in *C. andrewsiana* (fig. 21) than in *C. umbellulata* (fig. 20) and *C. uniflora* (fig. 17).

The micropylar nucleus remains at that end of the sac; the three smaller abortive nuclei migrate toward the chalazal end (fig. 18); later they may unite (fig. 19). The movement of the abortive nuclei may be aided by the

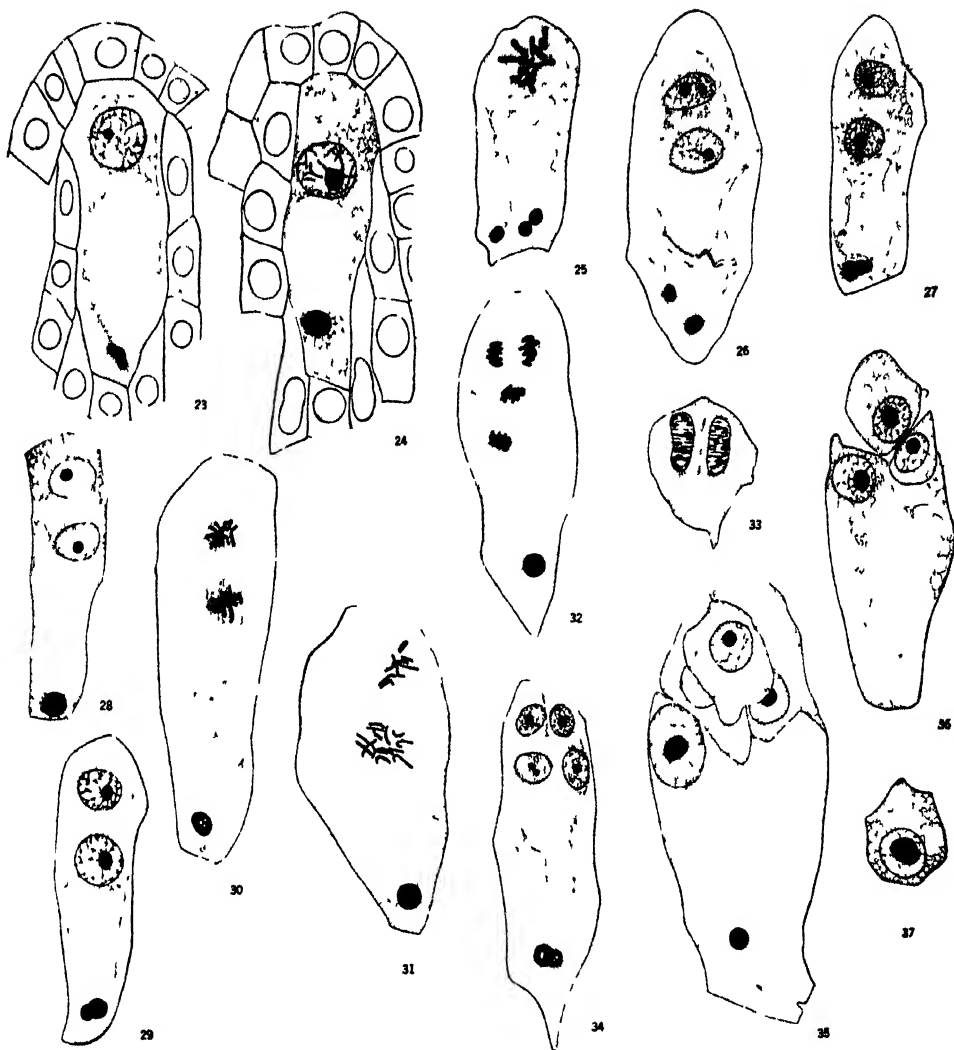


FIG. 23. Fusion of abortive nuclei in chalazal region embryo sac of *C. andrewsiana*. FIG. 24. The same in *C. uniflora*. FIG. 25. Polar view, equatorial plate, third nuclear division in embryo sac of *C. umbellulata*. Three abortive nuclei in chalazal region of sac. FIG. 26. Embryo sac of *C. umbellulata* after third division. Spindle fibers present. Abortive nuclei have migrated to chalazal region of sac. FIG. 27. The same. Abortive nuclei fuse. FIG. 28. The same in *C. uniflora*. FIG. 29. The same. Disappearance of spindle fibers. FIG. 30. Equatorial plates, fourth division in embryo sac of *C. umbellulata*. FIG. 31. The same in *C. uniflora*. FIG. 32. Anaphase of final division in embryo sac of *C. umbellulata*. FIG. 33. Cell plate formation between synergid nuclei of *C. uniflora*. FIG. 34. Mature embryo sac of *C. umbellulata*. FIG. 35. Mature embryo sac of *C. uniflora*. FIG. 36. The same for *C. andrewsiana*, showing synergid, egg, and primary endosperm cell. FIG. 37. Synergid of embryo sac shown in figure 36.

formation of the large central vacuole (figs. 19, 20, 21). Union of the nuclei occurs in various ways; in some sacs the two upper nuclei fuse before coming in contact with the third nucleus (fig. 19); while in others the two lower nuclei fuse first. Figures 22 and 23 show a single nucleus in which the lobes representing the abortive nuclei are still visible. Fusion of the nuclei may be delayed, however, until after the division of the functional megaspore nucleus (figs. 25, 26).

R. W. Smith has shown a stage in the union of abortive nuclei similar to figure 26. Such a figure has been interpreted by Maheshwari as possibly a secondary 4-nucleate stage, in which the two micropylar nuclei are haploid, the two chalazal nuclei being triploid as a result of the division of the 3 abortive nuclei on a common spindle. The absence of spindle fibers between the abortive nuclei, the difference in size and the variation in position of nuclei (figs. 19, 26) seem to make it clear that in my material the abortive nuclei are in a process of fusion and are not the result of division.

The functional megaspore nucleus rests for a time and then divides. The spindle during its division is usually parallel to the long axis of the embryo-sac and the two nuclei are formed one above the other (figs. 26, 27, 28). The first division occurs almost simultaneously in the two nuclei; the spindles of this division are approximately at right angles to each other as shown in figures 30, 31, and 32.

Upon completion of this division four nuclei are present at the micropylar end of the embryo-sac. Cell division occurs by cell plate formation (fig. 33). The two upper sister nuclei with surrounding cytoplasm become the synergids; the uppermost of the other pair with the surrounding cytoplasm becomes the egg, and the remaining one is the free polar nucleus of the primary endosperm cell (figs. 34, 35). The polar nucleus remains in position until fertilization occurs.

SUMMARY

The chromosome number of *Clintonia borealis* is $n = 16$, of *C. umbellulata* $n = 14$, of *C. andrewsiana* $n = 14$, and of *C. uniflora* $n = 14$.

The embryo-sac development in *C. umbellulata*, *C. andrewsiana*, and *C. uniflora* is similar to that described by R. W. Smith for *C. borealis*, and by F. H. Smith (3) for *C. uniflora*.

A single hypodermal cell is differentiated as an archesporial cell. This functions directly as the megaspore mother-cell.

As a result of meiosis, four megaspore nuclei are formed, an uppermost large rounded nucleus and three smaller undifferentiated nuclei.

The smaller (abortive) nuclei usually migrate toward the chalazal end of the embryo-sac and may unite.

Two further divisions result in the formation of four nuclei from the

nucleus at the micropylar end of the embryo-sac. Cell division is by cell plate formation.

The mature embryo-sac consists of four cells; two synergids, an egg, and a primary endosperm cell containing a haploid nucleus and the remains of the abortive nuclei.

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STUDIES IN OHIO FLORISTICS—III. VEGETATION OF OHIO PRAIRIES¹

CLYDE H. JONES

When the early settlers crossed the Appalachian Mountains and came into the territory which now comprises the State of Ohio, they found numerous variations from the relatively unbroken forests through which they had been traveling.

In the central part of the state they found rather extensive areas, scattered through a dozen or more counties, which were dominated by grass vegetation. Without a doubt these were outliers of the tall grass prairie, that "vast sea of waving grasses" which dominated the landscape farther to the west (10). These central Ohio grasslands for the most part consisted of a complicated mosaic of grasslands interlaced with tree-bordered streams, swamp forests, swales, and isolated prairie groves on some of the better drained sites.

Between these outliers of the true prairie of the interior lowland and the forests of the plateau, there existed an irregular, discontinuous zone of small areas populated with prairie grasses and with forbs of the deciduous forest. A few examples of these diverse habitats are as follows: sand and clay ridges well within the plateau, such as the Buffalo Beats in Athens County and the Kettle Hills in Fairfield County; pre- and inter-glacial river valleys at the plateau margin, such as the floodplain prairie at Lancaster, Fairfield County, and the Higby Prairie of the abandoned preglacial valley south of Chillicothe, Ross County; bog margins, such as the marl bogs of Pickaway and Ross Counties; and the limestone and dolomite cliff-top prairies of the plateau escarpment, such as Buzzards Roost in Adams County.

For many years numerous questions pertaining to the age of the prairies have confronted the ecologist (2, 5, 8, 11, 12, 13). Today many of these same questions continue to challenge the student of Ohio prairies. Prairies located on the till-plains and moraines of the Wisconsin glacier were obviously post-Wisconsin in age, but the problem of age becomes much more complicated in relation to those areas within or at the edge of the plateau that were neither glaciated nor submerged during glaciation.

Closely associated with problems of age is the problem of migration routes over which the ancestors of these plants traveled. They may have migrated into Ohio during preglacial times over a widespread front of continuous habitats, many of which were undoubtedly destroyed later by the

¹ Papers from the Department of Botany, The Ohio State University, No. 456.

southward advance of the glaciers. If these plants were present in Ohio prior to the period of glaciation, it seems reasonable to believe that many of them could have survived on favorable sites in the unglaciated plateau during advances of the ice. During inter- and postglacial periods these plants could have then migrated into areas in the west-central part of the state. The rela-

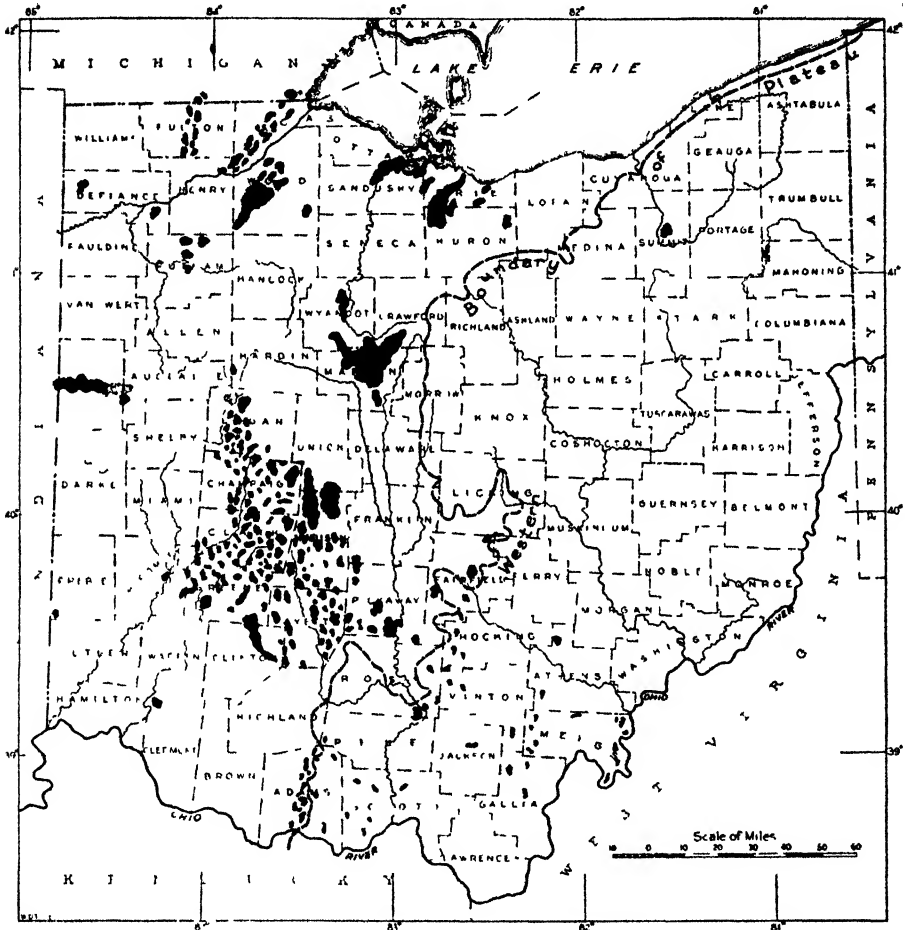


Fig. 1. Approximate location of the major prairie areas of Ohio. Size of individual areas exaggerated. Adapted from E. N. Transeau's *Prairie Peninsula Map* (1935).

tive absence of extensive prairies in eastern Indiana gives credence to this speculation (4).

On the other hand, if the major migration of prairie plants into the state was from the west in postglacial times, it must have been mainly over the newly exposed Wisconsin till-plains and moraines since few prairie plants

have been found on the ancient Illinoian till-plains in Ohio, as has been pointed out by Braun (1).

The relative absence of prairie plants on the Illinoian till-plains gives rise to interesting speculations in relation to the date of migration and the migration routes of the ancestors of the prairie plants which now occupy the dry prairie sites in Adams County. The possibility of their having migrated into this area prior to Illinoian glaciation has been suggested by Braun (1). It is altogether possible, however, that this migration could have occurred from the Wisconsin till-plains to the north in postglacial times along exposed limestone formations, slack-water silts, or the plateau margin itself. Another possibility is that of a northeastern migration from the "Kentucky Barrens" region which could have occurred in pre-, inter-, or post-Pleistocene times.

When one studies the distribution of the following prairie plants on glacial till-plains and moraines in Illinois (7), Indiana (4), and Ohio as well as on unglaciated areas in Kentucky (6), West Virginia (3), and Ohio, these problems become even more complicated, and one is inclined to believe that this migration may have occurred over any one or all three of the suggested routes.

Acerates floridana
Acerates viridiflora
Andropogon furcatus
Andropogon scoparius
Asclepias tuberosa
Bouteloua curtipendula
Brauneria purpurea
Calatula atriplicifolia

Cassia Chamaecrista
Eryngium yuccifolium
Liatris spicata
Liatris squarrosa
Lithospermum canescens
Panicum virgatum
Silphium trifoliatum
Sorghastrum nutans

The main purpose of this paper, however, is to present a list of the plants which occurred on the prairie areas of Ohio at the time of settlement. As one might expect, this is not an easy task, since agricultural operations and pasturing during the intervening period of years have completely destroyed or at least greatly altered the original vegetation of all the known prairie locations. Numerous remnants of the prairie vegetation remain, fortunately, on roadsides, fence rows, abandoned cemeteries and school grounds, sand dunes, steep moraines, ridge tops, and cliff edges within these areas. An analysis of the relative abundance of species within these areas leads one to believe that the following major grassland types (14) were well represented in Ohio: Big Bluestem, Little Bluestem, Slough Grass, and Tall Panic Grass—Wild Rye.

According to historical records, the grasses of the *Andropogon furcatus*-dominated grasslands of the deep, moist, black soil areas of central Ohio grew in such luxuriance that the early settlers had to stand up in their saddles to locate the grazing cattle (9). Poorly drained sites within these areas, such as sloughs and swales, were dominated by *Spartina Michauxiana*, and sand

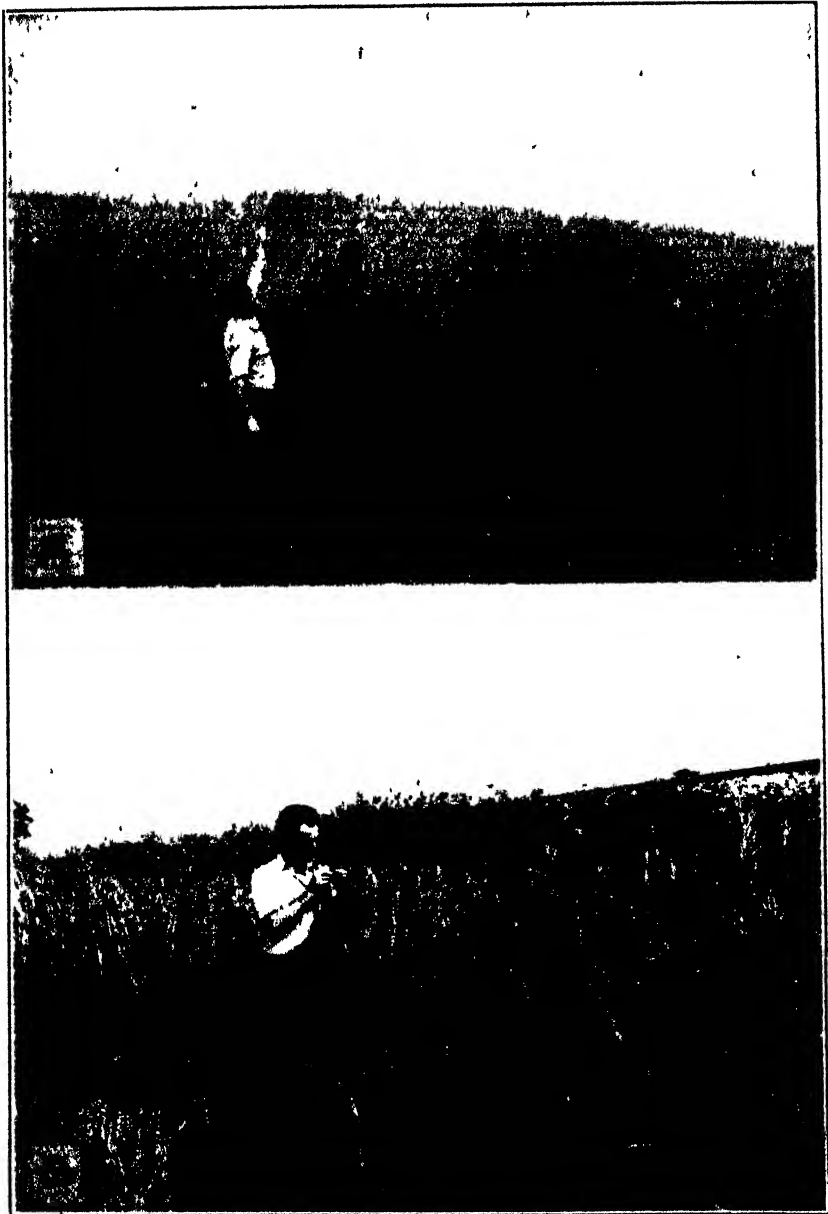


FIG. 2. A. A prairie area dominated by *Andropogon furcatus*, Adams County. B. A prairie slough dominated by *Spartina Michauxiana*, Marion County.

ridges and moraines were covered with *Andropogon scoparius*. The overdrained and over-exposed "meadow and glade" areas within and at the edge of the plateau were dominated by *Andropogon scoparius* and *Sorghastrum*

nutans, which frequently grew as bunch grass instead of forming closed associations as did the *Andropogon furcatus* on the flat areas in the central part of the state. Locally, especially on sites located on calcareous materials, *Andropogon furcatus*, *Andropogon scoparius*, *Sorghastrum nutans*, and *Bouteloua curtipendula* were dominant.

The following list of plants is believed to be representative of the species characteristic of Ohio's prairies.² It contains plants which were collected from numerous, diverse prairie habitats in the state, and it is quite unlikely that any single original prairie contained all of the species listed.

Dominants	
<i>Andropogon furcatus</i>	<i>Sorghastrum nutans</i>
<i>Andropogon scoparius</i>	<i>Spartina Michauxiana</i>
Subdominants	
<i>Acerates floridana</i>	<i>Filipendula rubra</i>
<i>Acerates viridiflora</i>	<i>Gaura biennis</i>
<i>Ambrosia bidentata</i>	<i>Gentiana puberula</i>
<i>Amorpha fruticosa</i>	<i>Gerardia tenuifolia</i>
<i>Arenaria patula</i>	<i>Geum canadense</i>
<i>Artemisia gnaphalodes</i>	<i>Habenaria leucophaca</i>
<i>Artemisia ludoviciana</i>	<i>Hedeoma hispida</i>
<i>Asclepias Sullivantii</i>	<i>Helianthus grosseserratus</i>
<i>Asclepias tuberosa</i>	<i>Helopsis scabra</i>
<i>Asclepiodora viridis</i>	<i>Houstonia angustifolia</i>
<i>Aster azureus</i>	<i>Houstonia lanceolata</i>
<i>Aster Drummondii</i>	<i>Hypericum cistifolium</i>
<i>Aster laevis</i>	<i>Isanthus brachiatus</i>
<i>Aster salicifolius</i>	<i>Juncus interior</i>
<i>Aster Tradescantii</i>	<i>Koeleria cristata</i>
<i>Bidens aristosa</i>	<i>Kuhnia eupatorioides</i>
<i>Bouteloua curtipendula</i>	<i>Kuhnia glutinosa</i>
<i>Brauneria purpurea</i>	<i>Lechea stricta</i>
<i>Cacalia atriplicifolia</i>	<i>Lepachys columnaris</i>
<i>Cacalia tuberosa</i>	<i>Lеспедеза capitata</i>
<i>Carex crus-corvi</i>	<i>Liatris cylindracea</i>
<i>Carex suberecta</i>	<i>Liatris scariosa</i>
<i>Cassia Chamaecrista</i>	<i>Liatris spicata</i>
<i>Cassia nitilans</i>	<i>Liatris squarrosa</i>
<i>Cirsium discolor</i>	<i>Lilium michiganense</i>
<i>Cleome serrulata</i>	<i>Lilium superbum</i>
<i>Croton monanthogynus</i>	<i>Linum sulcatum</i>
<i>Desmanthus illinoensis</i>	<i>Lithospermum canescens</i>
<i>Desmodium canadensis</i>	<i>Monarda mollis</i>
<i>Elymus canadensis</i>	<i>Muhlenbergia capillaris</i>
<i>Equisetum kansanum</i>	<i>Muhlenbergia cuspidata</i>
<i>Equisetum laevigatum</i>	<i>Muhlenbergia racemosa</i>
<i>Erigeron pulchellus</i>	<i>Oenothera speciosa</i>
<i>Erigeron ramosus</i>	<i>Panicum huachucae</i>
<i>Eryngium yuccifolium</i>	<i>Panicum Scribnerianum</i>
<i>Erysimum asperum</i>	<i>Panicum virgatum</i>
<i>Euphorbia corollata</i>	<i>Plantago Purshii</i>

² Nomenclature essentially that of Gray's Manual, 7th edition.



FIG. 3. A prairie area of central Ohio as it appears today. Madison County.

Prenanthes aspera
Prenanthes racemosa
Pycnanthemum pilosum
Pycnanthemum virginianum
Rosa blanda
Rosa Lyonii
Rosa setigera
Rudbeckia sp. ciosa
Rudbeckia Sullivanti
Sabatia angularis
Sanicula greqaria
Scutellaria parvula
Senecio plattensis
Silene regia

Silphium terbinthinaceum
Silphium terbinthinaceum
 var. *pinnatifidum*
Silphium trifoliatum
Solidago ohioensis
Solidago Kiddellii
Sphenopholis obtusata
Sporobolus asper
Sporobolus clandestinus
Syntherisma Bullii
Thalictrum dioicum
Trifolium stoloniferum
Verbena bracteosa
Vernonia missouriensis

Viola pedatifida

The following list represents plants which frequently occur in association with these prairie dominants at the edge of forests and on over exposed and over drained areas such as cliff tops, sand and clay ridges, gravel moraines, and porous calcareous material

Agrimonia mollis
Amphicarpa monica
Aster cordifolius
Aster laevis
Aster oblongifolius
Aster sagittifolius
Aster undulatus

Baptisia australis
Baptisia leucantha
Bignonia capricollata
Ceanothus ovatus
Chrysopsis graminifolia
Comandra umbellata
Coreopsis tripteris

¹ Confined for the most part to habitats derived from calcareous material

Desmodium bracteosum
Desmodium illinoense
Eupatorium sessilifolium
Galactia volubilis
Helianthus microcephalus
*Hexalectris spicata*³
Hypericum gentianoides
*Leavenworthia uniflora*³
Lechea racemulosa
Lobelia leptostachys
*Manfreda virginica*³
Ophioglossum Engelmannii
Panicum Boscii
Pentstemon lucvigatus
 var. *digitalis*
*Phaseolus polystachyus*³
*Phlox glaberrima*³
Plantago aristata
Polygala sanguinea

Polygala verticillata
 var. *ambigua*
Prenanthes altissima
Psoralea Onobrychis
Psoralea pedunculata
Ruellia ciliosa
Solidago bicolor
Solidago erecta
Solidago rigida
Solidago speciosa
 var. *angustata*
Spiranthes Beckii
Spiranthes gracilis
Stylosanthes biflora
*Thalictrum revolutum*³
Thaspium pinnatifidum
Viola lanceolata
Viola sororia
*Viola Walteri*³

The following list represents plants of general distribution which frequently occur in these prairie areas.

Agrimonia mollis
Amphicarpa monica
Anemone canadensis
*Anemone virginiana*⁴
Antennaria plantaginifolia
Apocynum androsaemifolium
Apocynum cannabinum
Asclepias incarnata
Aster multiflorus
Aster novae-angliae
Carex pennsylvanica
Carex vulpinoidea
Cinna arundinacea
Dodecatheon Meadia
*Eragrostis pectinacea*⁴
Erigeron ramosus
Eragaria virginiana
*Galium concinnum*⁴
Galium tinctorium
Glyceria nervata
Helianthus giganteus
Helianthus grosseserratus
Helianthus hirsutus
Helianthus tuberosus
Heliopsis helianthoides
Hypoxis hirsuta
Juncus tenuis
Juncus Torreyi
Leerna oryzoides
Leersia virginica
Leptandra virginica

Lobelia cardinalis
Lycopus americanus
Lythrum alatum
Monarda fistulosa
Muhlenbergia mexicana
*Muhlenbergia Schreberei*⁴
Oenothera biennis
*Oralis stricta*⁴
*Oralis violacea*⁴
Phalaris arundinacea
Physalis lanceolata
Physalis virginiana
Poa pratensis
Polygonum Muhlenbergii
Potentilla canadensis
Pycnanthemum flexuosum
Rhus toxicodendron
*Rosa virginiana*⁴
Rudbeckia hirta
Ruellia strepens
*Sanicula marilandica*⁴
Senecio aureus
*Senecio obovatus*⁴
*Smilax hispida*⁴
Solanum carolinense
Solidago canadensis
Solidago nemoralis
*Solidago ulmifolia*⁴
Specularia perfoliata
Steironema ciliatum
Steironema quadriflorum

³ Confined for the most part to habitats derived from calcareous material.

⁴ Confined for the most part to dry habitats.

Teucrium canadense
Thalictrum dasycarpum
Verbena angustifolia
Verbena hastata

• *Verbena stricta*
Vernonia altissima
Zizia aurea
Zizia cordata

Trees and shrubs of the following list frequently border dry prairie areas or occur as scattered specimens within these areas.

Celtis occidentalis
Cercis canadensis
Cornus florida
Cornus paniculata
Corylus americana
Diospyros virginiana
Fraxinus americana
*Fraxinus quadrangulata*⁴
Gaylussacia baccata
Juniperus virginiana
Liriodendron tulipifera
Ostrya virginiana
Pinus rigida
Pinus virginiana
Prunus americana

Quercus coccinea
Quercus marilandica
*Quercus Muhlenbergii*⁵
Quercus stellata
Quercus velutina
Rhamnus caroliniana
Rhus canadensis
Rhus copallina
Rhus glabra
Salix humilis
*Thuja occidentalis*⁵
Ulmus americana
Ulmus fulva
Vaccinium vacillans
Viburnum prunifolium

Dry prairie habitats are much more numerous and extensive within the plateau today than they were at the time of white man's occupation. Hundreds of acres of land on the narrow, steep-sided ridges were cleared and converted into farm lands. In a few years the farmers discovered that these areas could not be farmed profitably year after year because of over-drainage and lack of sufficient essential minerals in the soil. Eventually most of them were either abandoned or converted into pastures. As one might expect, the present-day vegetation cover of many of these tracts has been influenced by factors such as the following:

1. *Length of time area was under cultivation before abandonment.* For example, if the area was used exclusively for the production of cultivated crops for many years, the probability of the roots of the native perennials being eradicated is much greater than if the area was soon abandoned or converted into permanent pasture.

2. *Vegetation cover at the time of abandonment.* If there was a well-established grass cover at the time of abandonment, such as would be found in a meadow, the species that comprise the succeeding association will differ from those which would become established following a cultivated crop such as corn.

3. *Pasture history.* One area under observation had been pastured rather lightly for many years by sheep, and the dominant association consisted of *Andropogon virginicus* and *Danthonia spicata*. The area was then subjected

⁴ Confined for the most part to dry habitats.

⁵ Confined for the most part to habitats derived from calcareous materials.

to heavy grazing by cattle, and in three years the most conspicuous association consisted of *Aristida dichotoma*, *Hypericum punctatum*, *Solanum carolinense*, and *Achillea millefolium*.

4. *Organic content of the soil at the time of abandonment.* When the soil of these upland areas has been depleted of organic material, a xeric condition tends to come into being, which in turn limits the types of vegetation which can become established.

5. *Location of the area in relation to plants producing seed.* In numerous instances *Pinus rigida*, *Pinus echinata*, and *Pinus virginiana* have become

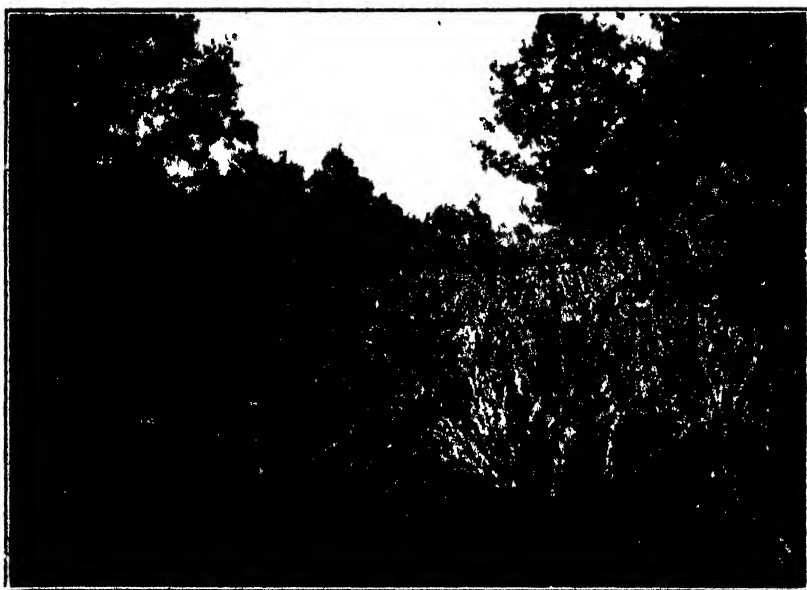


FIG. 4. A typical dry prairie within the plateau. Available information indicates that this area has not been plowed or pastured. The dominant grasses are *Andropogon scoparius*, *Andropogon furcatus*, and *Sorghastrum nutans*. Athens County

established in abandoned pastures near woodlots containing seed trees of these species.

6. *Chemical composition of the soil.* *Sorghastrum nutans*, for example, is much more likely to become established on areas deficient in calcium than *Bouteloua curtipendula*.

7. *The direction and degree of land slope.* Areas sloping towards the south or towards the direction of the prevailing winds are usually much dryer than those which slope towards the north or away from the prevailing winds. Likewise, if the slope is steep, excessive water runoff will result, bringing into being conditions which favor the establishment of the more xeric species.

8. *The degree to which the surface soil was removed before abandonment.* When most of the surface soil has been removed by the agents of erosion before abandonment, the area is limited in its capacity to support a great variety of species. Likewise, plant succession is retarded when this condition exists.

The following plant successions, however, are representative of the vegetation changes which frequently occur on these abandoned areas. The different stages and the dominant species of each are presented in the sequence A, B, and C.

1. Abandoned meadow (cultivated grasses) followed by:

A	B	C
<i>Aster ericoides</i> var. <i>villosus</i>	<i>Danthonia spicata</i> <i>Aristida dichotoma</i>	<i>Andropogon virginicus</i> <i>Andropogon scoparius</i>
<i>Eragrostis cilianensis</i> <i>Eragrostis pectinacea</i> <i>Panicum capillare</i> <i>Gnaphalium obtusifolium</i> <i>Rumex acetosella</i> <i>Achillea millefolium</i> <i>Daucus carota</i>	<i>Solidago nemoralis</i>	<i>Tridens flavus</i>

2. Abandoned grain field (corn, wheat, or oats) followed by:

A	B	C
<i>Digitaria sanguinalis</i> <i>Ambrosia elatior</i> <i>Echinochloa Crus-galli</i> <i>Setaria viridis</i> <i>Setaria lutescens</i> <i>Solanum carolinense</i>	<i>Aster ericoides</i> var. <i>villosus</i> <i>Erigeron ramosus</i> <i>Erigeron philadelphicus</i> <i>Apocynum cannabinum</i> <i>Convolvulus arvensis</i>	<i>Solidago nemoralis</i> <i>Aster ericoides</i> var. <i>villosus</i> <i>Smilax glauca</i> <i>Rubus villosus</i>

In addition to the species listed in the above successions and the scattered specimens such as were listed for the original prairies, the following herbaceous plants frequently occur in these disturbed areas.

<i>Acalypha gracilens</i> <i>Acalypha virginica</i> <i>Agrostis alba</i> <i>Antennaria plantaginifolia</i> <i>Aster Shortii</i> <i>Chrysanthemum Leucanthemum</i> <i>Cirsium lanceolatum</i> <i>Dianthus Armeria</i> <i>Dipsacus sylvestris</i> <i>Draba verna</i> <i>Echium vulgare</i> <i>Hedeoma pulegioides</i> <i>Hieracium scabrum</i> <i>Houstonia ciliolata</i> <i>Houstonia longifolia</i> <i>Hypericum punctatum</i> <i>Lactuca canadensis</i>	<i>Lactuca scariola</i> <i>Linaria vulgaris</i> <i>Lobelia inflata</i> <i>Lysimachia terrestris</i> <i>Panicum latifolium</i> <i>Physalis heterophylla</i> <i>Plantago aristata</i> <i>Plantago lanceolata</i> <i>Plantago major</i> <i>Poa compressa</i> <i>Prenanthes altissima</i> <i>Prunella vulgaris</i> <i>Sericocarpus asteroides</i> <i>Solidago juncea</i> <i>Sonchus asper</i> <i>Sonchus oleraceus</i> <i>Verbascum thapsus</i>
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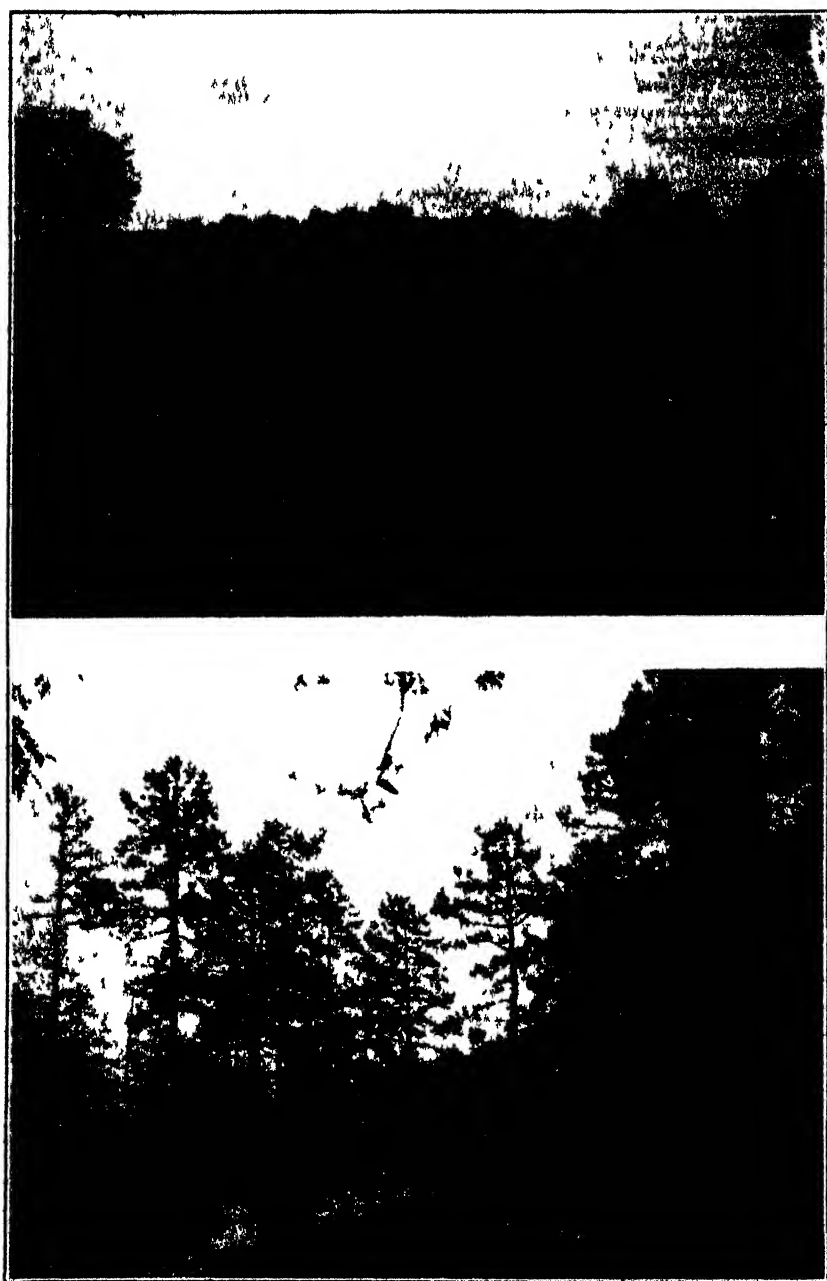


FIG. 5. A. A dry prairie area corn field within the plateau five years after abandonment. Galia County. B. Fifty years ago this dry prairie area was a corn field. Meigs County.

The preceding grasses and forbs, however, seldom dominate these dry prairie areas for long. Usually in about five years, clumps of *Rubus allegheniensis* and scattered sprouts and seedlings of some of the following trees and shrubs begin to appear in various combinations.⁶

Carya cordiformis
Carya glabra
Carya microcarpa
Carya ovata
Cercis canadensis
Corylus americana
Crataegus sp.
Diospyros virginiana
Fragaria americana
Liriodendron tulipifera
Nyssa sylvatica
Pinus echinata

Pinus rigida
Pinus virginiana
Prunus serotina
Quercus coccinea
Quercus stellata
Quercus velutina
Rhus copallina
Rhus glabra
Robinia pseudo-acacia
Sassafras variifolium
Ulmus americana
Ulmus fulva

When these trees and shrubs begin to form closed associations, the grasses and forbs lose dominance rapidly, and in a few years the area which was once occupied by a secondary prairie becomes dominated by mixed deciduous or mixed deciduous-southern pine associations.

Thus man has played diverse roles in relation to the prairies of Ohio. In some parts of the state he has destroyed or greatly altered the existing vegetation of these areas. In others he has been the indirect cause of secondary prairies, prairies which frequently exist for only a few years and are then succeeded by the invading forest.

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EFFECT OF DIFFERENT CONCENTRATIONS OF SYNTHETIC AUXINS ON DECAPITATED SUNFLOWER STEMS

SALLY KELLY

The object of the following work was to determine the concentrations at which synthetic auxins were effective in inducing gall formation, epinasty, and bud inhibition on decapitated sunflower stems. Using the same test plant, Gustafson (4) found that one per cent mixtures in lanolin of indoleacetic, indolebutyric, and phenylacetic acids caused galls at the point of application, and all but the latter inhibited the growth of lateral buds. Blum (2), applying 0.2 per cent solutions in lanolin of indoleacetic, indolebutyric, indolepropionic, naphthaleneacetic, and phenylacetic acids to decapitated sunflower stems, also found that all substances tested caused galls; all but indolepropionic and phenylacetic acids inhibited lateral bud development, and all but phenylacetic acid produced epinasty. These authors did not attempt to determine threshold concentrations required to produce the observed effects.

METHODS

Seeds of *Helianthus annuus* L. were planted in river sand contained in separate pots and watered biweekly with a full nutrient solution. After seven weeks' growth, the plants were decapitated about one inch above the second node. Twelve plants were used per concentration. Controls consisted of both decapitated and undecapitated plants. Plain lanolin was applied to the stump of the decapitated controls. The plants tested with indoleacetic (IAA) and indolebutyric (IBA) acids were planted October 18. Indolepropionic (IPA), phenylacetic (PAA), and naphthaleneacetic acid (NAA) treated plants were planted April 1. The auxins were dissolved in anhydrous lanolin and smeared over the entire cut surface of the stumps in approximately equal dosages. Four applications were made at five-day intervals, the previous lanolin applications being removed at the time of the new application. Between applications the compounds were stored at 2° C. The effective concentration range for each substance was determined in preliminary experiments. The final concentrations used are shown in table 1.

RESULTS

Bud Inhibition. In figure 1 are summarized the data obtained on the effect of auxins on inhibition of lateral bud growth. After three weeks, growth of lateral buds of plants treated with the highest concentrations of NAA and IBA was completely inhibited, whereas the lateral buds of those

TABLE 1. *Concentrations of synthetic auxins^a applied in lanolin to decapitated sunflower stems*

Per cent concentration in lanolin				
IAA	IBA	NAA	PAA	IPA
0.004	0.002	0.002	0.111	0.008
0.012	0.006	0.006	0.333	0.024
0.037	0.018	0.018	1.0	0.074
0.111	0.056	0.056	5.0	0.222
0.333	0.167	0.167	10.0	0.667
1.0	0.5	0.5	15.0	2.0
3.0	1.5	1.5	20.0	6.0

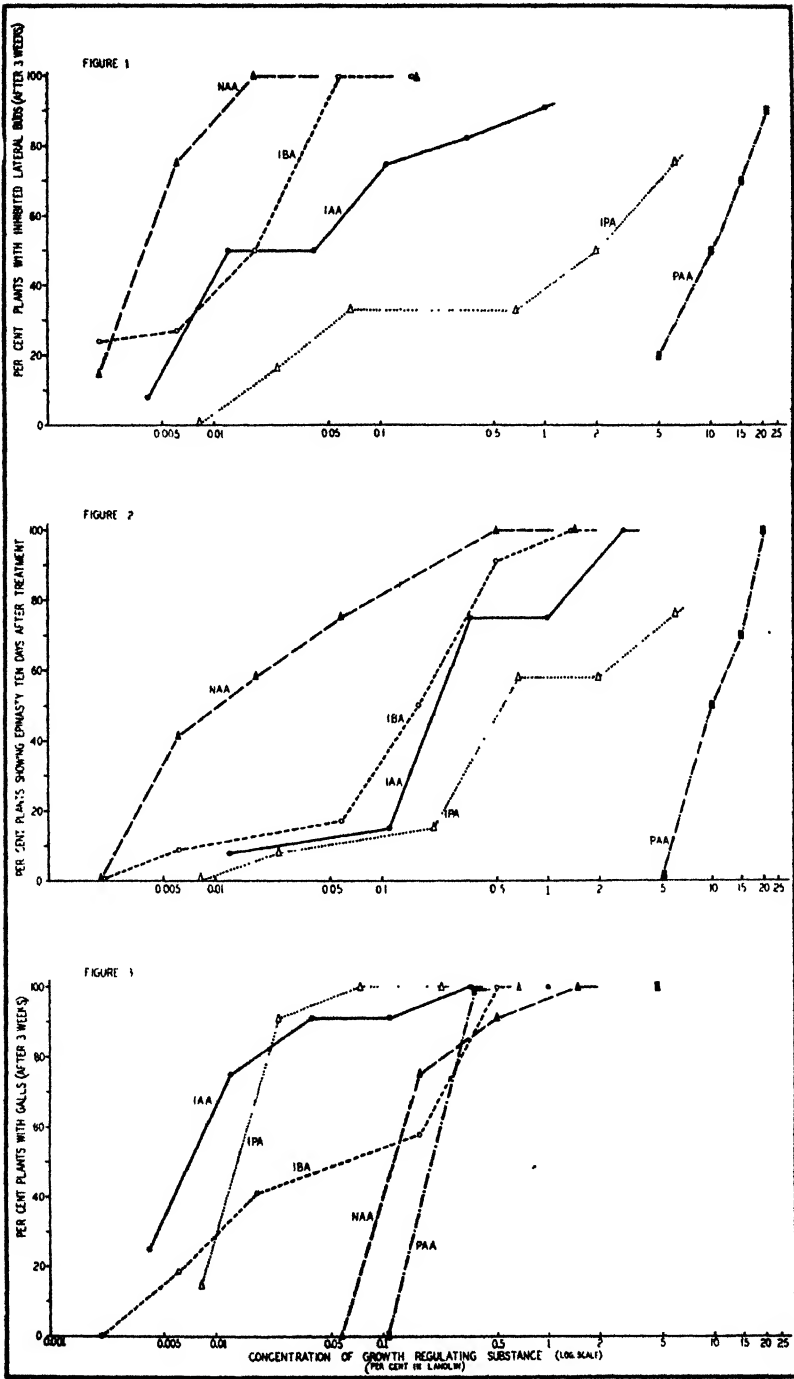
^a All compounds were obtained from the Dow Chemical Company, or from Merck and Company.

treated with the highest concentrations of the other auxins were only partially inhibited. The data indicate that (a) threshold concentrations of the various auxins differ; and (b) the relative activities of the various auxins differ according to whether they are compared at concentrations required to produce threshold response (15 to 20 per cent of plants with bud inhibition) or 50 per cent response. Thus, for IBA, NAA, IAA, IPA, and PAA, threshold responses were obtained at 0.002, 0.002, 0.005, 0.024, and 5.0 per cent, respectively. Concentrations necessary to produce 50 per cent inhibition were 0.018, 0.004, 0.033, 2.0, and 10.0 per cent, respectively.

Gall Formation. Gall formation occurred in 100 per cent of the plants (at the point where auxin was applied) when these were treated with high concentrations of the substances (fig. 3). The highest concentrations of IAA and IBA (table 1) produced browning and shriveling of the stem at the point of application, and concentrations of 10 per cent or more of PAA destroyed the tissues completely. The largest galls were produced by the following: IAA at 1.0 per cent, IBA at 1.5, IPA at 2.0, NAA at 1.5, and PAA at 5.0 per cent. Galls resulting from IPA and IAA applications were the largest of all. Concentrations necessary to produce threshold responses (15 to 20 per cent of plants with detectable galls) were found to be of approximately the same order for IAA, IBA, and IPA, approximately ten times greater for NAA, and thirty-five times greater for PAA. With certain concentrations of IAA, IPA, and PAA, galls developed on individual plants, even though lateral bud growth was not inhibited in these same plants. Thus the concentrations in which auxins are effective in producing galls do not always correspond to

Explanation of figures 1-3

FIGS. 1-3. Comparative effect of varying concentrations of synthetic auxins on bud inhibition, epinasty, and gall formation in sunflower. Concentrations are plotted on a logarithmic scale for the sole purpose of getting so wide a range into a single figure. FIG. 1. Bud inhibition, 3 weeks after first treatment. FIG. 2. Epinastic responses, ten days after first treatment. FIG. 3. Gall formation, 3 weeks after first treatment.



those producing bud inhibition. In the lower concentrations IPA is relatively more effective in producing galls than in inhibiting lateral buds; on the other hand, NAA is more effective in producing bud inhibition than galls.

Stem thickening occurred below the second node in plants treated with the high concentrations of NAA.

Epinasty. Plants receiving the highest concentration of each substance gave epinastic responses within from one to five days after the first application. In general, the concentrations necessary to bring about threshold epinastic responses, as measured after ten days (fig. 2), were higher than those for bud inhibition and gall formation. The relative activities of the various auxins are approximately the same whether they are compared at concentrations required to produce threshold or 50 per cent responses. This is in contrast with bud inhibition effects, where the relative activities of the auxins differed at threshold and 50 per cent responses. Epinasty produced in plants by higher auxin concentrations was more pronounced than by lower concentrations.

DISCUSSION

The approximate relative activities of the various auxins are summarized in table 2. For ready comparison IAA is arbitrarily assigned a value of 100

TABLE 2. *Approximate relative activities of synthetic auxins determined by comparison of the concentrations in lanolin which bring about threshold and 50 per cent responses.*

In this study concentrations of indoleacetic acid are arbitrarily assigned a value of 100 for each response.

Auxin	Bud inhibition		Gall formation		Epinasty		Avena curvature ^a
	Threshold response (A)	50 per cent response (B)	A	B	A	B	
Indoleacetic acid	100	100	100	100	100	100	100
Indolebutyric acid	250	100	67	11	200	200	4
Indolepropionic acid	20	0.9	50	110	50	34	0.08 ^b
Naphthalenetic acid	250	450	6	11	3000	2400	18
Phenylacetic acid	0.1	0.2	2	3	2	2	0.002 ^b

^a Data from Avery, Berger, and Shalucha (1), unless otherwise indicated.

^b From Went and Thimann (6).

for both threshold and 50 per cent responses; the relative activities of the other auxins are expressed in terms of those of IAA. Thus it may be seen that NAA was the most effective substance in producing bud inhibition and epinasty, and IAA was the most effective gall former. Gustafson (5) also

found NAA to be an effective gall-former on both tomato and sunflower plants. In this connection it is interesting to note that Braun and Laskaris (3) have reported NAA and IBA to be more effective than IAA in stimulating tumor growth on tomato stems previously inoculated with an attenuated strain of *Phytophthora tumefaciens*. IPA was the least active indole compound producing bud inhibition and epinasty in this study, and it is also known to be the weakest in producing *Avena* curvature. It is about as active in gall formation as the other indole compounds. Gustafson (5) found no such gall-forming activity for IPA in his tests. PAA, which at 1 per cent concentration failed to cause bud inhibition in Gustafson's work, was found to inhibit buds at concentrations of 5 per cent and higher. In all responses measured it is less active than the other auxins.

The data obtained in this study confirm and extend the general conclusion in the literature, namely, that the relative effectiveness of different auxins varies according to the type of response which is measured, even on the same test plant.

SUMMARY

1. Synthetic auxins dissolved in lanolin and applied to the decapitated stumps of sunflowers produced three responses: lateral bud inhibition, gall formation, and epinasty. Naphthaleneacetic acid also produced stem thickening below the second node.

2. The concentrations necessary to bring about gall formation and bud inhibition were lower, in general, than those necessary to produce epinasty, when measured ten days after the first application.

3. At threshold concentrations, naphthaleneacetic acid (0.002 and 0.006 per cent) was most effective in producing bud inhibition and epinasty; and indoleacetic acid (0.004 per cent) was the most effective gall-former. As compared with NAA, IBA was less effective in inhibiting lateral buds and more effective in producing galls. Indolepropionic acid produced large galls but was not especially effective in producing the other two responses. Except in higher concentrations, phenylacetic acid was ineffective in producing bud inhibition and epinasty; 0.3 per cent produced galls, but concentrations of 10 per cent and higher destroyed the plant tissues.

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THOMAS JEFFERSON HIS INTEREST IN PLANT LIFE AS REVEALED IN HIS WRITINGS*—I

EDMUND H. FULLING

The amazing versatility of Thomas Jefferson has been much extolled by his biographers, and numerous have been the eulogies inspired by it. As a political philosopher of the early American republic, Jefferson will always stand preeminent, and to him in the future there will be attributed, as in years gone by, many a political concept that seeks the authority of great men become venerable through their wisdom and the passage of time. In other fields of intellectual endeavor he was scarcely less astute, and in his grasp of great principles and simultaneous devotion to details, he displayed an "exquisite mind, which was both telescopic and microscopic in its range and operations" (7).

It is because of this amazing versatility, encompassing many fields of science, particularly an enduring interest in plant life, that another contribution is here offered to the already voluminous literature upon the life of this great statesman. Most previous biographical sketches of Jefferson have at least recognized his life-long concern with agriculture, and a few have emphasized his broader interests in plants. Among the latter are accounts of his relation to botany (27), of his gardening activities (4, 28) and, most recently, of his relation to all sciences of his time, including agriculture, botany and horticulture (6).¹ Despite these excellent treatises there is in his writings evidence of still greater interest in the vegetable world than has so far been recognized, other than by cursory allusion. It is the purpose of the present study to unite, in some measure, these hitherto unemphasized discourses of Jefferson with those which have already been revealed, and thus to provide in botanical literature a more inclusive account of Jefferson's role as agriculturist, botanist, and gardener.

Considered thus in their entirety, Jefferson's writings on plants give us not only a better understanding of the man himself but also an assemblage of data possessing historical value from purely agricultural and botanical standpoints. This is particularly true with respect to plants of economic value. Jefferson's interest in all branches of science was primarily utilitarian, and the introduction of useful plants as well as improved agricul-

* Prepared in partial fulfillment of an Act of Congress to commemorate the two hundredth anniversary of the birth of Jefferson.

¹ This scholarly article was published as a "prereprint" shortly after the present study was begun. In a large measure, it considers phases of Jefferson's interests previously recorded only in his own writings, and unavoidably mentioned again and even cited in the present account.

tural practices were constant concerns of his. Nevertheless, the present contribution is essentially biographical; its principal objective is to reveal something of the personality of a great man as his phenomenal mentality penetrated into nearly every branch of human knowledge.

To that end, impersonal paraphrasing of his writings is deliberately avoided; instead, abundant quotations from his works are cited. It is only through such quotations and not by the words of another author in feeble attempts to describe them that a reader may secure his own realistic impressions of one unknown to him personally, and not merely the impressions of a eulogistic biographer. Furthermore, there are so many interesting details in the writings of a man like Jefferson, that any one attempting to embody them accurately in a new rendition inevitably must resort to citations. Ample evidence is at hand that others, too, have come to this conclusion, for there have already been published various compilations of choice selections from his writings on a variety of topics, including agriculture, a comprehensive two-volume assemblage of which will appear shortly under Government imprint.

Jefferson was a phenomenally prolific writer, not of "books" or of articles for publication—he strictly adhered to a policy of never writing for the "press"—but of letters, 40,000 pieces of which in 236 volumes repose today among his manuscripts in the Library of Congress, with an additional 10,000 in 67 volumes in the library of the Massachusetts Historical Society (2). Other papers are in the custody of the Huntington Library, San Marino, California; the Pennsylvania Historical Society; the Missouri Historical Society; and the University of Virginia. Some 325 letters of this voluminous correspondence deal with agricultural matters. When it is borne in mind that this prodigious personal correspondence was carried on in longhand and that Jefferson preserved a duplicate of most of it, made by means of moistened paper or an ingenious polygraph of his own design and construction, one marvels, to say the least, at the astounding industry of the man.

A major portion of this correspondence has been published in three large works, one of nine (11), another of ten (12) and the third of 20 volumes (13), none of which has been regarded as wholly satisfactory, either quantitatively or qualitatively. To remedy this situation there is now in preparation a definitive edition of the papers of Thomas Jefferson, to include not only all his available writings but also all preserved letters written to him, and to comprise some 50 volumes. It is under the editorship of Julian Boyd, historian and librarian of Princeton University, and will be published by the Princeton University Press. Some idea of the enormous variety of topics which this monumental work will cover may be gained from the encyclopedia of 1900 founded upon the ten-volume edition; that compendium assembles

quotations from Jefferson's writings under 9,228 headings (16). One wonders, indeed, what the index to the contemplated 50 volumes will offer by way of subject matter. The present paper is based almost wholly on the 20-volume edition, whence almost all the quotations given have been extracted.

In addition to the many references to plant life in his correspondence, Jefferson left for posterity among his meticulously kept account books, two detailed records which also are of great interest to us, his "Farm Book" and his "Garden Book." The former was begun in 1774 and continued until 1822; the latter, started in 1766 and continued, except during his absence, until 1824. Both of them have hitherto been only in manuscript form. This year, however, the American Philosophical Society, of which Jefferson at one time was president, has published an annotated edition of the "Garden Book" under the editorship of Professor E. M. Betts of the University of Virginia, who has been instrumental in the restoration of Jefferson's gardens at Monticello; and the "Farm Book" may be included in the contemplated Government edition of all Jefferson's agricultural writings, already referred to.

I. AGRICULTURE

INTRODUCTION

Thomas Jefferson was a member of the landed gentry in colonial Virginia, in the days when young America was still primarily an agricultural country. By inheritance of more than 2,000 acres from his father and by subsequent purchases of his own, he became the proprietor, by 1794 and at the age of 51, of 10,647 acres. This area, according to his "Farm Book," consisted of 15 parcels of land, several of which made up his Albemarle estate of 5,591 $\frac{1}{2}$ acres wherein was included his now famous home of Monticello, on a mountaintop overlooking and about three miles from the town of Charlottesville. Less than 1,200 acres of this Albemarle holding was ever cleared of trees and put under cultivation, and on another parcel, of more than 4,000 acres, known as Poplar Forest, only about 800 acres came under the axe. One of the smallest parcels, of only 157 acres, was in wilderness and contained what today is one of the "shrines" of America and at which Jefferson long hoped to build a retreat for himself—the Natural Bridge of Virginia.

That Jefferson's heart and soul were always in Monticello and the surrounding country and that his 40 years² in statecraft were but an interlude in his preferred preoccupations with his farms and garden, is attested by many references in his correspondence to the day when he might return to

² From his election to the House of Burgesses of the Colony of Virginia in 1769 to his retirement from the Presidency in 1809.

them. He began construction on Monticello in 1770, managed his farms for 14 years, and in 1784, after the turmoil of the Revolution, was sent to Europe with Franklin and Adams to negotiate commercial treaties with European powers. The next year he succeeded Franklin as American representative to France, and did not return to America until 1789. During the intervening years, while residing in Paris, he accommodated himself to the pomp and circumstance of a regal court, serving his country but ever thinking of his Albemarle estate. Four years before the termination of his tenure in that office he confessed to a French acquaintance:

"I am savage enough to prefer the woods, the wilds, and the independence of Monticello, to all the brilliant pleasures of this gay Capital. I shall, therefore, rejoin myself to my native country, with new attachments, and with exaggerated esteem for its advantages; for though there is less wealth there, there is more freedom, more ease, and less misery."

Upon his return to America, four years later, Jefferson entered Washington's cabinet as the first American Secretary of State but retired from that position the last day of 1793. In 1794 he returned to Monticello and gave vent to his feelings when he wrote to Washington:

"I return to farming with an ardor which I scarcely knew in my youth, and which has got the better entirely of my love of study. Instead of writing ten or twelve letters a day, which I have been in the habit of doing as a thing in course, I put off answering my letters now, farmer-like, till a rainy day, and then find them sometimes postponed by other necessary occupations."

The next year, in writing to James Madison about his broken down health of the last eight months, he wrote on

"above all things, the delights I feel in the society of my family, and in the agricultural pursuits in which I am so eagerly engaged."

It was not many years, however, before his public services were again demanded by his country, this time as President of the United States. That his interest in agricultural matters never slackened during the eight years in that office is attested in several ways, perhaps the most interesting of which is his faithful formulation during all those years of a chart which showed the average earliest and latest dates of appearance in the Washington market of 36 varieties of vegetables. From this table we learn that Washingtonians of those days were supplied at various times during the year with

artichokes	broccoli	cauliflower
asparagus	cabbage	celery
beets	carrots	corn

³ Letter to Baron Geismar, September 6, 1785 (13, V, 127).

⁴ Letter to George Washington, April 25, 1794 (13, IX, 283).

⁵ Letter to James Madison, April 27, 1795 (13, IX, 301).

cress	mushrooms	sorrel
cucumbers	parsley	spinach
currants	parsnips	sprouts
eggplant	peas	squash
endive	potatoes	strawberries
grapes	radishes	tomatoes
lettuce	raspberries	turnips
lima beans	salsifia	watermelon
melons	snapa	windsor beans

Two of Jefferson's biographers have reproduced this chart in their works (6, 24), and one of them, especially impressed by his devotion to details and ability to detach himself from the weighty matters of State, was induced to comment (24): "To think of a leader of a great civil revolution—the founder of a new party and creed—the statesman engaged in the pressing cares of a nation—watching with a green-grocer's assiduity, and recording with more than a green-grocer's precision, the first and last appearance of radishes, squashes, cabbages, and cauliflowers in the market—suggests a curious train of reflections."

It would be unfortunate, indeed, were Jefferson's formulation of that chart to do no more than "suggest a curious train of reflections"; it should serve, rather, as a precept to be emulated of unswerving interest despite the more urgent cares, faithfully discharged, which interrupted his devotion to a chosen avocation.

In 1808, when about to retire from those cares, we again find Jefferson longing for Monticello when he wrote to Chancellor Livingston, the eminent jurist and statesman, thanking him for certain volumes of *Agricultural Proceedings* and mentioning receipt of other proceedings from the *Agricultural Society of Paris*:

"Writings on this subject are peculiarly pleasing to me, for, as they tell us, we are sprung from the earth, so to that we naturally return. It is now among my most fervant longings to be on my farm, which, with a garden and fruitery, will constitute my principal occupation in retirement."⁶

And after consummation of this longing he wrote to an old classmate:

"I have withdrawn myself from all political intermeddlings, to indulge the evening of my life with what have been the passions of every portion of it, books, science, my farms, my family and friends."⁷

Agricultural pursuits were thus not merely incidental events in Jefferson's life; together with other phases of natural science, physics, chemistry, mechanics, and what not else, they ranked foremost in his thoughts, and earned for him the rather substantial income for those days of about \$2,000 per year. In company with Washington and others, he was one of the most

⁶ Letter to R. R. Livingston, January 3, 1808 (13, XI, 111).

⁷ Letter to James Maury, April 25, 1812 (13, XIII, 141).

progressive farmers of his time, so far as seeking improvements in techniques and crops was concerned, though not the most successful in yields obtained. To his farming practices he applied, with whatever modifications seemed necessary, the teachings of recognized agricultural authorities, and toward this end, we are told, he had in his extensive library, 78 volumes upon agriculture, 48 of which were in English, 24 in French, five in Italian and one in Latin (6).⁸

The details of these activities, minutely recorded in his "Farm Book," are obviously beyond consideration in a paper of the present size. Certain generalities, however, must not be overlooked in any treatment of the subject, and these will now be noted.

AGRICULTURAL ACTIVITIES AT MONTICELLO

Tobacco, Corn, and Wheat. For a great many years after the founding of Virginia by the first permanent English settlement at Jamestown in 1607, tobacco was the most important staple crop of the colonists, even the principal medium of currency at one period, and its culture was undertaken by practically every landowner, large and small. It long constituted the most valuable export of all the colonies, and from 1744 to 1776 the amounts shipped abroad averaged about 40,000,000 pounds per year. Jefferson, as a plantation owner, contributed to this production in the early days of Monticello, where at one time he was called master by 154 slaves. Tobacco was an important source of revenue to those who raised it, and on one occasion, at least, Jefferson expected to realize £50 sterling per hogshead on his produce.⁹

The usual routine of growing it in those days was to remove the forest from virgin land, to plant the weed for five successive years, and then to let the land lie fallow for a season or more, followed by a repetition of this sequence until the crop raised no longer was remunerative. Rotation of crops was generally not practiced, and manuring the land was out of the question to restore its pristine fertility after so wantonly destroying it by this barbaric spoliation; it was cheaper to buy new land, to clear it and to extend the ravaging husbandry.

There were a few thoughtful farmers, however, among them Washington and Jefferson, who condemned this exploitation and were quick to recognize that the heyday of Virginia tobacco was gradually fading after the three-quarter mark of the century. The market price was falling, cheaper

⁸ Though the inclusion of these volumes in Jefferson's library indicates his interest in plant life as well as do other phases of his activities, they will not be enumerated or further discussed here because they are not among his writings. For an interesting commentary upon them, the reader is referred to Dr. Brown's article (6). It must be mentioned, however, that Jefferson's library, purchased by Congress in 1815, became the nucleus of the present Library of Congress after the original was burned.

⁹ Letter to Thomas Adams, February 20, 1771 (13, IV, 229).

lands had to be sought elsewhere, and long before he returned to Monticello in 1794 Jefferson abandoned cultivation of the exhausting weed on his Albemarle estate. In his "Notes on the state of Virginia," published ten years earlier in Paris, he remarked:

"In the year 1758 we exported seventy thousand hogsheads of tobacco, which was the greatest quantity ever produced in this country in one year. But its culture was fast declining at the commencement of this war¹⁰ and that of wheat taken its place; and it must continue to decline on the return of peace. I suspect that the change in the temperature of our climate has become sensible to that plant, which to be good, requires an extraordinary degree of heat. But it requires still more indispensably an uncommon fertility of soil; and the price which it commands at market will not enable the planter to produce this by manure. Was the supply still to depend on Virginia and Maryland alone as its culture becomes more difficult, the price would rise so as to enable the planter to surmount those difficulties and to live. But the western country on the Mississippi, and the midlands of Georgia, having fresh and fertile lands in abundance, and a hotter sun, will be able to undersell these two States and will oblige them to abandon the raising of tobacco altogether. And a happy obligation for them it will be. It is a culture productive of infinite wretchedness. Those employed in it are in a continual state of exertion beyond the power of nature to support. Little food of any kind is raised by them; so that the men and animals on these farms are badly fed, and the earth is rapidly impoverished."¹¹

In lieu of tobacco Jefferson advocated that

"The cultivation of wheat is the reverse in every circumstance. Besides clothing the earth with herbage and preserving its fertility, it feeds the laborers plentifully, requires from them only a moderate toil except in the season of harvest, raises great numbers of animals for food and service, and diffuses plenty and happiness among the whole. We find it easier to make an hundred bushels of wheat than a thousand weight of tobacco and they are worth more when made."¹¹

This substitution of crops did not, however, preserve the fertility of his lands, for during his ten years' absence from Monticello his overseers practiced a rotation which exhausted the soil probably more though less rapidly than did tobacco. They sowed wheat and maize in alternate years in the virgin soil of newly cleared land between the stumps of felled trees, and repeated this rotation so long as they could get five bushels of wheat or ten bushels of corn per acre. This system was followed probably under the influence of John Taylor, an exceptionally good farmer of Caroline County, Virginia, "whose bountiful crops bore witness to the merits of his teachings." Taylor argued strongly in favor of maize as the alternate crop in preference to the English dependence on turnips, peas and potatoes. After the yield of wheat or Indian corn no longer was remunerative, the land was aban-

¹⁰ War between France and England.

¹¹ (13, II, 237).

doned and new areas cleared for similar exploitation; all of which offered little improvement over the previous era of tobacco culture.

Jefferson was Secretary of State at this time, keeping an eye on his declining farms as best he could, and attempting to remedy matters by engaging proper overseers. Two years before returning to Monticello he hired one Samuel Biddle as superintendent, who was willing to undertake the job for \$120 per year, wages which were a good deal higher than Jefferson expected to pay. In his instructions to Biddle, Jefferson furnished us some particulars when he wrote to him that

"The farm is of about five or six hundred acres of cleared land, very hilly, originally as rich as any highlands in the world but much worried by Indian corn & tobacco. It is still however very strong, & remarkably friendly to wheat & rye. These will be my first object. Next will be grasses, . . . & the introduction of potatoes for the use of the farm, instead of Indian corn, in as great a degree as possible. . . . I have long banished tobacco, & wish to do the same by Indian corn in a great degree."¹²

At the same time Jefferson had an area of 2,000 acres which he wanted to rent in parcels of not less than 200 acres at 25¢ per acre, but always with restrictions against growing too much Indian corn. On this point he wrote in his "Farm Book," under the heading "Tenants":

"Tie them up to some rotation of crops which shall include ameliorating years to counterbalance at least the exhausting ones,"

and to Mr. Freeman, in charge of Monticello, he wrote with respect to one lessor:

"I understand this tenant has tended the same ground in corn both the years he has lived on it. He must therefore go off unless he will put the whole of it into wheat now, or oats in the spring. If he does not, we must put it in oats in the spring . . ." (24).

President Washington, at this time, was in correspondence with the eminent English agricultural writer, Arthur Young, concerning problems of his own. Jefferson appears to have shared in the exchange of letters, and in commenting to the President upon some of Young's recommendations, he indicates the contemplated changes in agricultural practice which he soon adopted:

"Good husbandry with us consists in abandoning Indian corn and tobacco, tending small grain, some red clover following, and endeavoring to have, while the lands are at rest, a spontaneous cover of white clover. I do not present this as a culture judicious in itself, but as *good* in comparison with what most people there pursue. Mr. Young has never had an opportunity to see how slowly the fertility of the *original soil* is exhausted. With moderate management of it, I can affirm that the James river lowgrounds with the cultivation of small grains, will never be exhausted; because we

¹² Letter to Samuel Biddle, December 12, 1792 (13, XVIII, 189).

know that under that cultivation we must now and then take them down with Indian corn, or they become, as they were originally, too rich to bring wheat. The highlands, where I live, have been cultivated about sixty years. The culture was tobacco and Indian corn as long as they would bring enough to pay the labor. Then they were turned out. After four or five years rest they would bring good corn again, and in double that time perhaps good tobacco. Then they would be exhausted by a second series of tobacco and corn. Latterly we have begun to cultivate small grain; and excluding Indian corn, and following, such of them as were originally good, soon rise up to fifteen or twenty bushels the acre. . . . I mean in a farm of about 500 acres of cleared land and with a dozen laborers to try the plan of wheat, rye, potatoes, clover, with a mixture of some Indian corn with the potatoes. . . ."¹³

About a year later, in again writing to Washington about the depleted state of his farms, he was induced by further inspection of them to exclaim:

"Ten years' abandonment of them to the ravages of overseers, has brought on them a degree of degradation far beyond what I had expected."¹⁴

Jefferson's Rotation of Crops as a Final Effort to Restore the Depleted Fertility of His Soil. In a final effort to rescue his land from utter destruction as a result of incompetent management during his absence abroad, Jefferson adopted a new plan of crop rotation in 1794 when he returned to Monticello. He divided the 1,120 acres under cultivation into four farms of 280 acres each, and each farm into seven fields of 40 acres, marking the boundaries by rows of peach trees, of which he set out 1,151 that first year. The seven fields indicated the basic nature of the new system, a seven-year rotation, and each farm, under its own overseer, was cultivated by four negroes, four negresses, four horses and four oxen. The precise sequence of crops which Jefferson followed in this new scheme apparently varied somewhat, for the many references to it in his correspondence indicate changes from year to year. As related to John Taylor, the agricultural authority of the time, it was as follows: first year—wheat, followed that same year by turnips to be fed to the sheep; second year—corn and potatoes in alternate rows, followed in autumn by winter vetch to be used in the spring as fodder, if so wanted, or to be turned in; third year—peas or potatoes, or both, according to the quality of the field; fourth year—rye or wheat with clover; fifth and sixth years—clover, turned in the autumn of the latter and followed by vetch; seventh year—the vetch plowed under in the spring, buckwheat sown and turned in later, followed by autumn wheat to begin the cycle again.

Jefferson's agricultural correspondence contains abundant references to this system of rotation, to its modifications, its merits and its results. It is in that same letter to Taylor, however, that we find perhaps the best expression of his concern with it and of his understanding in the matter:

¹³ Letter to George Washington, June 28, 1793 (13, IX, 139).

¹⁴ Letter to George Washington, May 14, 1794 (13, IX, 286).

"And though I observe your strictures on rotations of crops, yet it appears that in this I differ from you only in words. You keep half your lands in culture, the other half at nurse; so I propose to do. Your scheme indeed requires only four years and mine six; but the proportion of labor and rest is the same. My years of rest, however, are employed, two of them in producing clover, yours in volunteer herbage. But I still understand it to be your opinion that clover is best where lands will produce them. Indeed I think that the important improvement for which the world is indebted to Young is the substitution of clover crops instead of unproductive fallows; and the demonstration that lands are more enriched by clover than by volunteer herbage or fallows; and the clover crops are highly valuable. That our red lands which are still in tolerable heart will produce fine clover I know from the experience of the last year; and indeed that of my neighbors had established the fact. And from observations on accidental plants in the fields which have been considerably harrassed with corn, I believe that even these will produce clover fit for soiling of animals green. I think, therefore, I can count on the success of that improver. My third year of rest will be devoted to cowpeaning, and to a trial of the buckwheat dressing. A further progress in surveying my open arable lands has shewn me that I can have seven fields in each of my farms where I expected only six; consequently that I can add more to the portion of rest and ameliorating crops. I have doubted on a question on which I am sure you can advise me well, whether I had better give this newly acquired year as an addition to the continuance of my clover, or throw it with some improving crop between two of my crops of grain, as for instance between my corn and rye. I strongly incline to the latter, because I am not satisfied that one cleansing crop in seven years will be sufficient; and indeed I think it important to separate my exhausting crops by alternations of ameliorators. With this view I think to try an experiment of what Judge Parker informs me he practices. That is, to turn in my wheat stubble the instant the grain is off, and sow turnips to be fed out by the sheep. But whether this will answer in our fields which are harrassed, I do not know. We have been in the habit of sowing only our freshest lands in turnips, hence a presumption that wearied lands will not bring them. But Young's making turnips to be fed on by sheep the basis of his improvement of poor lands, affords evidence that though they may not bring great crops, they will bring them in a sufficient degree to improve the lands. I will try that experiment, however, this year, as well as the one of buckwheat. I also attended to another improver mentioned by you, the winter vetch, and have taken measures to get the seed of it from England, as also of the Siberian vetch which Millar greatly commends, and being a biennial might perhaps take the place of clover in lands which do not suit that. The winter vetch I suspect may be advantageously thrown in between crops, as it gives a choice to use it as green feed in the spring if fodder be run short, or to turn it in as green-dressing.

I am for throwing the whole force of my husbandry on the wheat-field, because it is the only one which is to go to market to produce money. Perhaps the clover may bring in something in the form of stock. The other fields are merely for the consumption of the farm. Melilot, mentioned by you, I never heard of. The horse bean I tried this last year. It turned out nothing. The President has tried it without success. An old English farmer of the name of

Spuryear, settled in Delaware, has tried it there with good success; but he told me it would not do without being well shaded, and I think he planted it among his corn for that reason. But he acknowledged our pea was as good an ameliorator and a more valuable pulse, as being food for man as well as horse. The succory is what Young calls *Chicoria Intubus*. He sent some seed to the President, who gave me some, and I gave it to my neighbors to keep up till I should come home. One of them has cultivated it with great success, is very fond of it, and gave me some seed which I sowed last spring. Though the summer was favorable it came on slowly at first, but by autumn became large and strong. It did not seed that year, but will the next, and you shall be furnished with seed. I suspect it requires rich ground, and then produces a heavy crop for green feed for horses and cattle. I had poor success with my potatoes last year, not having made more than 60 or 70 bushels to the acre. But my neighbors having made good crops, I am not disheartened. The first step towards the recovery of our lands is to find substitutes for corn and bacon. I count on potatoes, clover, and sheep. The two former to feed every animal on the farm except my negroes, and the latter to feed them, diversified with rations of salted fish and molasses, both of them wholesome, agreeable, and cheap articles of food."

After discussing the possibilities of a "movable airy cow house, to be set up in the middle of the field which is to be dunged," Jefferson continues:

"... observe that the turnips and two dressings of vetch do not cost a single ploughing. The turning the wheat-stubble for the turnips is the fallow for the corn of the succeeding year. The first sowing of vetches is on the corn (as is now practised for wheat), and the turning it in is the flush-ploughing for the crop of potatoes and peas. The second sowing of the vetch is on the wheat fallow, and the turning it in is the ploughing necessary for sowing the buckwheat. These three ameliorations, then, will cost but a single harrowing each. On the subject of the drilled husbandry, I think experience has established its preference for some plants, as the turnip, pea, bean, cabbage, corn, etc., and that of the broadcast for other plants as all the bread grains and grasses, except perhaps lucerne and Saint foin in soils and climates very productive of weeds. In dry soils and climates the broadcast is better for lucerne and Saint foin, as all the south of France can testify."¹⁵

While Jefferson was thus a pioneer in adopting to America the new agricultural practices being developed in England, and especially in advocating elaborate rotation of crops and use of legumes, he was by no means either the only one or the first to do so. Two years earlier, Washington had also adopted a seven-year rotation, believing with Jefferson that potatoes improved the soil. It was the use of legumes, however, which seems to have been paramount in Jefferson's mind as a means of improving his soil, and several references to the plants in his letters reveal his satisfaction with them. From a letter to James Madison, for instance, we learn that in 1794 he sowed about 40 acres to them, 120 acres the next year, and planned to sow 160-200 acres yearly thereafter.¹⁶ On another occasion he claimed never to have seen finer

¹⁵ Letter to John Taylor, December 29, 1794 (13, XVIII, 192).

¹⁶ Letter to James Madison, April 27, 1795 (13, IX, 301).

clover than in some of his fields which had never been previously manured, and on which his rotation at the time was triennial: one year of wheat and two of clover in the strongest fields, or two of peas in the weaker, with maize and potatoes after every other rotation, i.e., once in seven years.¹⁷

Additional light is shed upon Jefferson's legume husbandry by a letter to Washington in which he first defended himself against the attempt of someone who "thought it worth his while to try to sow tares between you and me, by representing me as still engaged in the bustle of politics, and in turbulence and intrigue against the government." Jefferson had laid down as a rule for himself never to write a word for the public papers, and he claimed in this letter never to have departed therefrom in a single instance. It appears, however, that something did become public in a publication of the time and attributed to him, which he very much resented. Without naming the person, he suspected someone who had possessed all his and Washington's confidence, but in the copy of the letter which he retained, there was written in the margin, apparently at a later date, the name "General H. Lee." He then continued:

"But enough of this miserable tergiversator, who ought indeed either to have been of more truth, or less trusted by his country.

I put away this disgusting dish of old fragments, and talk to you of my peas and clover. As to the latter article, I have great encouragement from the friendly nature of our soil. I think I have had, both the last and present year, as good clover from common grounds, which had several crops of wheat and corn without ever having been manured, as I ever saw on the lots around Philadelphia. I verily believe that a yield of thirty-four acres . . . has given me a ton to the acre at its first cutting this spring. The stalks extended, measured three and a half feet long very commonly. Another field, a year older, and which yielded as well the last year, has sensibly fallen off this year. My exhausted fields bring a clover not high enough for hay, but I hope to make seed from it. Such as these, however, I shall hereafter put into peas in the broadcast, proposing that one of my sowings of wheat shall be after two years of clover, and the other after two years of peas. I am trying the white boiling pea of Europe (the Albany pea) this year, till I can get the hog pea of England, which is the most productive of all. But the true winter vetch is what we want extremely."¹⁸

From England and Italy Jefferson received seed of winter vetch and all the good kinds of field pea grown in the former country. While he expected much from them and promised to send some to Taylor, should they succeed with him, he counted a good deal more, he wrote, on the southern cow-pea of the United States.¹⁹ Six months later he had occasion to thank some one for a box of seed, apparently from abroad, and commented that the peas and vetch contained in the consignment were most acceptable. They apparently

¹⁷ Anonymous letter, March 23, 1798 (13, X, 11).

¹⁸ Letter to George Washington, June 19, 1796 (13, IX, 339).

¹⁹ Letter to John Taylor, October 8, 1797 (13, XVIII, 201).

were of a variety already in cultivation in New York, but Jefferson expressed fear that the Virginia soil and sun were not suited to them. He wrote that a recent acquisition of cow-peas had pretty well supplied the place in his husbandry which he had destined for the European field pea. The role of legumes in nitrogen fixation was unknown to Jefferson, and this lack of knowledge accounts for his writing of the cow-pea that it was a

"very productive, excellent food for man and beast, awaits without loss our leisure for gathering, and shades the ground very closely throughout the hottest months of the year. This with the loosening of the soil, I take to be the chief means by which the pea improves the soil."²⁰

While Jefferson thus saved his land from complete ruination through uninterrupted cultivation of tobacco and maize, he apparently was always willing to return to them should they ever show signs of becoming profitable in a rising market, and to Taylor he wrote after four years rehabilitation work:

"The high price of tobacco, which is likely to continue for some time, has tempted me to go entirely into that culture, and in the meantime, my farming schemes are in abeyance, and my farming fields at nurse against the time of my resuming them."²¹

Years later, when his lands had presumably recovered some of their former fertility, he wrote in a rather cheerful vein that the vicinity of Charlottesville was excellently adapted to wheat, maize and clover; that garden peas, which were then being planted, came to the table about May 12, strawberries and cherries at about the same time, and asparagus around April 1. Artichoke stood the winter without cover, lettuce and endive with a slight cover. Figs, protected by a little straw, began to ripen in July; otherwise, not until September. The culture of the neighboring people was of wheat for market, of maize, oats, peas and clover for support of the farm. He informed his correspondent that it was regarded as good practice to divide a farm into three fields, putting one in wheat, half a one in maize, the other half in oats or peas, and the third in clover, tending the fields successively in this rotation. The best farmers, such as Mr. Randolph, his son-in-law, got 10 to 20 bushels of wheat per acre; the worst, as himself, 6 to 18.²²

Other Crops. According to his "Farm Book," in 1812 Jefferson cultivated at Monticello, 32 kinds of vegetables along with 22 crops and 13 varieties of grass. Each of them, very obviously, cannot be discussed in the limits of this article. From his correspondence, however, we learn that at one time he attempted to raise flax but found it so injurious to his lands and of such scanty reward that he discontinued its cultivation. Hemp, on the other hand,

²⁰ Anonymous letter, March 23, 1798 (13, X, 11).

²¹ Letter to John Taylor, November 26, 1798 (13, X, 63).

²² Letter to Jean Batiste Say, March 2, 1815 (13, XIV, 258).

was abundantly productive and, in his estimation, would grow forever on the same spot. In endeavoring to produce it, however, he found the breaking and beating of it, which was always done by hand, so slow and laborious and so much complained of by his laborers, that he gave it up, and purchased and manufactured cotton for their shirting. He did, however, devise a way of attaching a hemp-break to a threshing machine in an endeavor to revive its cultivation.²³

Grape vines, too, had their place in Jefferson's program, but by 1822 when some one made inquiry about a certain kind which Jefferson had, so many of the vines had died and others been replaced that he no longer knew one from the other. He did say, however, that the Scuppernon wine of North Carolina, made from a variety of Fox grape, *Vitis vulpina*, from the basin of the Scuppernon river in that State, proved to him that as good wines would some day be made in America as in Europe.²⁴

As late as 1916 seeds could still be obtained in Iowa of what was yet known as the "snake cucumber," a curiosity not uncommon in the 1860's which attained a length of four to six feet. It was probably with reference to this same variety, or a forerunner of it, that Jefferson, only six months before his death, revealed his continued interest not only in untried crops but also in the possibilities of plant breeding, when he wrote about his failing health and

"to request further that you will procure for me and send in a letter by mail half a dozen seeds of these mammoth cucumbers. One of 4 f. 6 i. long, and another of 4f.5 $\frac{1}{2}$ should afford so many seeds as to spare a few to a beggar. Altho giants do not always beget giants, yet I should count on their improving the breed, and this vegetable being a great favorite of mine, I wish to take the chance of an improvement."²⁵

AGRICULTURAL OBSERVATIONS IN EUROPE

In the spring of 1787, while serving as American Minister in France, Jefferson made a rather extensive journey into the southern parts of that country and into northwestern Italy, partly for the purpose of visiting the famous watering place of Aix. In his characteristically detailed manner he assembled numerous notes of agricultural practices and of the local flora in the provinces and towns through which he passed. These accounts, though sketchy, provide us today with some interesting observations on conditions in France and Italy at the close of the eighteenth century, not only with respect to agriculture and related topics, but also regarding the physiography of the country, the people and their industries. They cover an amazing variety of topics, as did all of Jefferson's observations, and we can readily

²³ Letter to George Fleming, December 29, 1815 (13, XIV, 365).

²⁴ Letter to Samuel Maverick, May 12, 1822 (15, 270).

²⁵ Letter to Thomas Worthington, November 29, 1825 (15, 298).

imagine him rolling along the dusty or muddy roads of the country in the horse-drawn vehicles of those days, tarrying at wayside inns and subjecting their keepers or other townspeople to questioning for information on nearly every topic that one might think of. It is in his notes regarding plants, of course, that we are particularly interested, and from them we gather the following picture.²⁶

From Sens to Vermanton, in the province of Champagne, which has since been subdivided, the plains were in corn and the hills in vineyards. A few apple trees dotted the landscape, but there was none of any other kind. In Burgundy, one of the oldest viticultural districts of Europe, also subdivided since Jefferson's visit, there was more of interest and worthy of noting. All the hills were in corn^{26a}; there were scattered areas of forest and wood, and, more specifically, of broom,²⁷ whins²⁸ and holly,²⁹ as well as inclosures of what Jefferson called quick hedge. In Dijon he found the best round potatoes that he had ever seen.

At the time of his visit in Burgundy, the first week in March, the peasants were planting, pruning and sticking their vines. Whenever a new vineyard was made the vines were planted in gutters about four feet apart, and as the vines advanced the peasants lay them down. As the vines put out new shoots, they filled all intermediate spaces, until all trace of order was lost and only about one square foot of open soil remained about each plant. They began to yield good profits in five or six seasons and lived up to 150 years. Manufacture of the famous Burgundy wines as well as of other kinds in the regions through which he passed, and the economics of their production occupied much of Jefferson's attention, but his accounts of those aspects are beyond our immediate interest.

In Beaujolois, another former subdivision of France, Jefferson found very little forest, the hillside vineyards inclosed in dry stone walls and the plains in fields of corn. The rotation of crops practiced by the peasants involved wheat the first year, small grains plus red clover the second, and all clover the third. The spontaneous pasturage of green sward was known to the natives as "fromenteau." Jefferson was impressed by the combined cultivation of vines, trees and grain in this part of France. Rows of fruit trees were planted about 20 feet apart, and between them in the rows were espaliered vines four feet apart. The intervals were sown in grain and pasture in alternate years. In Dauphiné, he was told, vines were planted only at the roots of trees and permitted to climb the trees, a practice which, he wrote, spoiled both the fruit and the wine.

²⁶ "Memoranda taken on a Journey from Paris into the Southern Parts of France, and Northern of Italy, in the year 1787" (13, XVII, 153-236).

^{26a} Jefferson used the term "corn" in the Old World sense, i.e., as meaning "grain" and including wheat, rye, and barley.

²⁷ *Cytisus scoparius*.

²⁸ *Ulex europaeus*.

²⁹ *Ilex Aquifolium*.

Wild gooseberries at this time (second week in March) were in leaf, wild pear and sweet briar in bud, and in Lyons almond trees were in bloom.

In Dauphiné, another ancient province, Jefferson was struck by what he described as the savage aspect of the country along both sides of the Rhone. The hand of man had subdued the scene, he wrote, "by planting corn where there is little fertility, trees where there is still less and vines where there is none." In the neighborhood of Lyons there was more corn than wine; toward Tains, more wine than corn; and beyond the latter, the extensive plains of the Rhone, where best, were in corn, clover, almonds, mulberries and walnuts. There were also some oaks, the hills were in vines, and near Lyons, but not much afterwards, was a good deal of forest wood. Where the hills were quite in waste, as he described them, they were covered with broom, whins, box and some clusters of small pine. Almond was in general bloom (March 15-18) and willows were putting out their leaves.

At Pains there had formerly been olive trees, but since a great cold some years before had killed them, they had not been replaced.

In Montelimart, too, the peasants planted corn with their vines; they grew an abundance of potatoes and other vegetables; and used walnut oil with their salad. Here, as elsewhere in France, vineyards were fertilized with dung gathered along the roadside, the collecting of which constituted a form of trade.

In the Principality of Orange the plains of the Rhone, two or three leagues wide, were also in corn, clover and almonds, and it was here that the country of olives began. They were the only trees which Jefferson saw planted among the vines. On the hills, thyme grew wild.

In Languedoc forests were absent but cultivated crops included corn, clover, lucerne,³⁰ St. Foin,³¹ olives, mulberries, willows for firewood and hoops, and some almonds. In parts, the waste hills were covered with thyme, box and chêne-vert.³² At Nîmes the peasants were pruning their olive trees (March 23), a good specimen of which would yield 60 pounds of fruit and 15 pounds of oil. In 1767 a cold spell of a week had killed all the olive trees, but next year the roots produced sprouts. Horse chestnut and mulberry trees were leafing, apple trees and peas blossoming, and from the joints of the Pont du Gard wild figs were flourishing.

The country about Aix was luxuriant, waving in vines, pastures of green sward and clover. There were perfect groves of olive trees and mixed among them were corn, lucerne, and vines. Waste ground threw out thyme and lavender. Firewood of the peasants consisted of chêne-vert and willow, and

³⁰ Lucerne = alfalfa.

³¹ Sainfoin or Saintfoin, a forage crop grown to some extent today in the southern United States, is *Onobrychis viciifolia*, a segregate from *Hedysarum*.

³² *Quercus ilex*.

plantings of the latter were lopped every three years. The peasants made their bread half wheat, half rye, and ate it in the mornings with an anchovy or an onion. Their vegetables were always eaten with oil and vinegar, and they drank piquette, made by pouring hot water over the pomace of pressed grapes.

Marseille, too, was the center of great olive groves, interplanted with corn, vines, lucerne, mulberry, almond and willow. Jefferson was informed that the olive grew nowhere more than 30 leagues from the sea, but he doubted that this was true of Spain, Portugal, Asia, and Africa, and expected that it would not apply to America. This last thought was important, as we shall later note, in his attempts to introduce olive culture into his native land.

The finest figs of Europe, Jefferson informs us, grew about Marseille, and were known as "figues Marcelloises" or "les veritables Marcelloises," to distinguish them from others of inferior quality. The figs were formed on the trees around the first of April and would keep any length of time, whereas others would exude a sugar in the spring and become sour. The Marseille fig, Jefferson was told, would degenerate if transplanted into any other part of the country. There were also a few trees of a small seedless grape from Smyrna, and the best of all grapes for drying was known as "des Pauses." They were very large with a thick skin and much juice, growing best against walls of southern exposure.

Gathering mulberry leaves constituted another means of earning a living, and caper buds³³ had to be collected every day as they formed, a labor that was performed by women. Pistache, too, grew in the neighborhood but not so well, and the peasants ate the fruits in the milky state. By the middle of March the people were cutting asparagus; they had Windsor beans on April 4; the next day Jefferson saw strawberries and the Guelder rose in blossom. Raisins were first dipped in lye and then dried in the sun to preserve them. Aloe grew in the open ground.

Jefferson mentions oranges first in the little village of Olioules, outside Marseille, and around Cuges capers were abundantly cultivated. From Olioules to Toulon, figs were in the open fields, some with stems 15 inches in diameter. They generally forked near the ground but some had single stems five feet long. The plants were large as apricot trees, and the olive trees about the size of large apple trees. Corn and almonds, too, were grown, as well as capers. The latter were planted eight feet apart, and the fruits, as already mentioned, were gathered by women, beginning about the last of June and continuing until the middle of October. Each plant had to be picked every day, and they grew equally well in the best or worst soil, even

³³ Pickled flower buds of the caper bush, *Capparis spinosa*, have long been used as a condiment and ingredient of sauces in the Old World.

in walls where there seemingly was none. Their life-span was that of a man or longer. Peas were available through the winter, occasionally under shelter, and they had been so without shelter since March 25.

At Hières, in addition to the usual olives, mulberries, vines, figs and corn, there were also some flax and cherry trees. Groves of fruit trees extended two or three miles from the town to the sea, and in them were orange trees of two feet diameter one way, one foot the other, the contour of all the larger trunks being oval rather than circular. The largest trees were 20 feet tall and yielded about 6,000 oranges per year. The leaves of many and some trees themselves had been killed by cold the previous November. One garden which Jefferson visited had about 15,600 trees, eight to ten feet apart, which blossomed and bore fruit at the same time and in every stage all year round. The best fruit was that which was gathered in April and May. There were also palm trees in Hières, 20 or 30 feet tall, but they bore no fruit, and the King kept a botanical garden here, concerning which Jefferson does not give us any details.

Beyond Hières, in addition to the customary crops of the region, were hedges of pomegranate, sweet briar and broom, and a great amount of thyme was growing wild. At Antibes and Nice oranges were in the open, but in small high inclosures and were protected by the neighboring mountains. This was true also of the oranges at Olioules, and Jefferson was induced to write that the climate seemingly did not permit their cultivation without shelter anywhere on the French side of the Alps.

Beyond Nice, as Jefferson journeyed through the Maritime Alps into Italy, oranges were no longer to be seen, and the olive was lost a little above the village of Scarena on Mount Braus, to be met again on the other side a little above the town of Sospelo. Wherever there was sufficient soil, the land was terraced and in grain, and waste areas were either in two-leaved pines or denuded. Likewise, in crossing Mount Brois near Ciandola and Tende, olives were lost at a certain height but found again on the other side at the village of Breglio. On the lowland there were also corn, vines, mulberries, figs, cherries and walnuts. At the village of Fontan olives disappeared and chestnut trees began in good quantities. About Limone and Coni, wherever there was sufficient soil on the mountains, corn was cultivated "quite to the commencement of the snows" on the mountains. Waste parts were in two-leaved pines, lavender and thyme. The plains near Coni were in pastures, corn, mulberries, and some almonds, and along the rivers was a great deal of golden willow.

At this point in his notes Jefferson makes the following interesting observation:

"The southern parts of France, but still more the passage through the Alps, enable one to form a scale of the tenderer plants, arranging them

according to their several powers of resisting cold. Ascending three different mountains, Braus, Brois, and Tende, they disappear one after another; and descending on the other side, they show themselves again one after another. This is their order, from the tenderest to the hardiest. Caper, orange, palm, aloe, olive, pomegranate, walnut, fig, almond. But this must be understood of the plant; for as to the fruit, the order is somewhat different. The caper, for example, is the tenderest plant, yet being so easily protected, it is the most certain in its fruit. The almond, the hardiest plant, loses its fruit the oftenest, on account of its forwardness. The palm, hardier than the caper and the orange, never produces perfect fruit in these parts."³⁴

From the mountains to Turin the walnut was the tenderest tree that survived, and of it as well as of almond and mulberry trees there were only a few. Grapes were more abundant, but most plentiful were willows and poplars. Corn, clover, and small grass were mixed with them, and the rich soil of the country was generally infested with wild onions. At Racconigi there was some cultivation of corn, but what attracted Jefferson most is thus expressed in his own words:

"They have a method of planting the vine, which I have not seen before. At intervals of about eight feet, they plant from two to six plants of vine in a cluster. At each cluster they fix a forked staff, the plane of the prongs of the fork at a right angle with the row of vines. Athwart these prongs they lash another staff, like a handspike, about eight feet long, horizontally, seven or eight feet from the ground. Of course, it crosses the rows at right angles. The vines are brought from the foot of the fork up to this cross piece, turned over it, and conducted along over the next, the next, and so on, as far as they will extend, the whole forming an arbor eight feet wide and high, and of the whole length of the row, little interrupted by the stems of the vines, which being close around the fork, pass up through hoops, so as to occupy a space only of small diameter."³⁵

Continuing on through other towns to Vercelli, cultivation of corn, pasture, maize, vines, mulberries, walnuts, willow and poplar continued. The peasants made hedges of willow by setting the plants one to three feet apart and bending them down to interlace with one another when they were eight or ten feet tall. None of these hedges appeared very old to Jefferson, and he concluded therefore that they soon died.

The Italian rice fields began in the neighborhood of Vercelli, whence Jefferson procured seed, as later related, for introduction into South Carolina. He noted that the water with which the fields were irrigated was very clear and that sowing of rice within two miles of cities was not permitted, on account of "insalubrity." Notwithstanding, Jefferson wrote, when the water was drawn off the fields in August, the whole country became subject to agues and fevers. The peasants estimated that the same measure of

³⁴ (13, XVII, 187.)

³⁵ (13, XVII, 188.)

ground yielded three times as much rice as wheat, and with half the labor. They were sowing their rice at the time of Jefferson's visit, April 19, and as soon as sowed, the fields were flooded, two or three inches deep. Six weeks or two months later, the water was drawn off to permit weeding. The fields were then flooded again and allowed to remain so until August, three or four weeks before the grain was ripe. In September the rice was cut, threshed, beaten in mortars to separate the husks, and then sifted into different qualities.

From Vercelli to Novara the fields were all in rice and mostly under water, and the dams separating several ponds were planted with willows. There were some figs in well-protected spots in Novara, but from there to Ticino the country was, for the most part, stony and waste, grown up in broom. From Ticino to Milan all was in corn, interplanted with willows, many mulberries, some walnuts, and here and there an almond. Nearing Milan, Jefferson was induced to write:

"They have still another method here of planting the vine. Along rows of trees, they lash poles from tree to tree. Between the trees are set vines, which, passing over the pole, are carried on to the pole of the next tree, whose vines are in like manner brought to this, and twined together, thus forming the intervals between the rows of trees alternately into arbors and open spaces. They have another method also of making quick-set hedges. Willows are planted from one to two feet apart, and interlaced, so that every one is crossed by three or four others."³⁶

Figs and pomegranates, Jefferson was told, grew unsheltered in Milan, but seeing none, he supposed they were rare. Olives had formerly grown there, but since a great cold in 1709 had killed them, they had not been replaced. In fact, the nights that Jefferson was in Milan, April 21 and 22, the rice ponds froze half an inch thick. Such ponds were not permitted within five miles of this city, and the intervening country was in corn, pastures, gardens, mulberries, willows and vines.

Butter and Parmesan cheese manufacture centered about Lodi and are carefully described in Jefferson's notes, one interesting detail of which is that an ounce of saffron, the dye secured from the dried, orange-colored stigmas of the locally native *Crocus sativus*, was added to seven brenta [brenta = 50 liters] of milk to give color to the cheese. [An ounce of saffron requires the stigmas of more than 4,000 flowers.]

At Novi the Apennines began to rise, their growth consisting of oak and chestnut. Walnut was soon lost in ascending the mountains but found again about one-fourth of the way down the other side. Half-way down, figs and vines were met, continuing in great abundance to the lowland. Between the mountains and Genoa, olive culture began again, and in the

immediate environs of the city were strawberries, figs, oranges, mulberries, and corn. Aloe grew in many places but never flowered.

Near Oneglia were many trees known as carroubier which Jefferson knew had been named *Ceratonia siliqua* by Linnaeus, a name that is still valid. These trees were, of course, the well-known carobs whose pods, as Jefferson learned, furnished food for horses, and also for the poor peasants in times of scarcity. At St. Remo orange and lemon trees were in abundance, and farther along toward Monaco and Nice were extensive plantations of palm trees. The midribs of these palms, Jefferson wrote, were in such demand in Rome on Palm Sundays, that cultivation here to meet that demand was a profitable enterprise.

Later, in France again, Jefferson found St. Foin extensively cultivated around Montpellier and known there as sparsette. There was also a great deal of madder or garance, *Rubia tinctorum*, the raising of which was said to be immensely profitable. In Jefferson's words:

"The first four years of madder are unproductive; the fifth and sixth yield the whole value of the land. Then it must be renewed. The sparsette is the common or true St. Foin. It lasts about five years; in the best land it is cut twice, in May and September, and yields three thousand pounds of dry hay to the setterie the first cutting, and five hundred pounds the second. . . . Lucerne is the best of all forage; it is sowed here in the broad-cast, and lasts about twelve or fourteen years. It is cut four times a year, and yields six thousand pounds of dry hay at the four cuttings, to the setterie."³⁷

In Certe, wine manufacture was the principal industry, as in most of the adjacent country, and it furnished great quantities of grape pomace for making verdigris.³⁸ At Carcassonne flax was in bloom (May 18) and Windsor beans had just come to the table, but there were not yet either strawberries or peas. At one point in this vicinity Jefferson noted what he said were the last olive trees, and in his memoranda he indulged in the following discussion with himself, so characteristic of his inquiring mind and devotion to detail:

"On a review of what I have seen and heard of this tree, the following seem to be its northern limits. Beginning on the Atlantic, at the Pyrenees, and along them to the meridian of la Lande, or of Carcassonne; up that meridian to the Cevennes, as they begin just there to raise themselves high enough to afford it shelter. Along the Cevennes, to the parallel of forty-five degrees of latitude, and along that parallel (crossing the Rhone near the mouth of the Isere) to the Alps; thence along the Alps and Apennines, to what parallel of latitude I know not. Yet here the tracing of the line becomes

³⁷ (13, XVII, 207.)

³⁸ Verdigris is a green pigment, known to the ancient Romans, used in dyeing and medicine, and much produced in the wine districts of France by exposing thin strips of copper to acetic acid developed in the residues from wine factories.

the most interesting. For from the Atlantic, so far, we see this production the effect of shelter and latitude combined. But where does it venture to launch forth unprotected by shelter, and by the mere force of latitude alone? Where for instance does its northern limit cross the Adriatic? I learn that the olive tree resists cold to eight degrees of Reaumur below the freezing point, which corresponds to fourteen above zero of Fahrenheit; and that the orange resists to four degrees below freezing of Reaumur, which is twenty-three degrees above zero of Fahrenheit."³⁹

This concern of Jefferson in wanting to know where latitude alone permitted olive cultivation was not merely academic; it had a very practical bearing, and, as we shall soon note, Jefferson later instructed Edward Rutledge to secure additional information on the subject, for he was interested in promoting olive culture in America.

The vineyards and production of wine in the neighborhood of Bordeaux occupy several pages of Jefferson's notes. In the surrounding country he found vines, corn, maize, farouche,⁴⁰ clover, lucerne, apples, cherries, and waste areas in furze⁴¹ and broom.

At Nantes, Carolina rice, a topic to be discussed later in considerable detail, was preferred to that of Lombardy for the Guinea trade because it required less water to boil.

Ascending the Loire from Nantes, Jefferson found the countryside as far as Angers in grain, pasture, vines, some maize, flax, and hemp. Beyond Nantes there were, in addition, many willows, poplars, and walnuts. The flax was nearly ripe (June 8), and sweetbriar was generally in bloom. There was still some broom on which the cattle and sheep browsed in winter and spring when they had no other green food. Hogs ate the blossoms and pods in spring and summer. The first crop of hay was being cut, and with a passing remark upon vineyards and wine production in the region, Jefferson concluded his agricultural observations on this journey in 1787.

The next spring he visited the Rhineland, but his notes from that journey are devoted primarily to other matters than plant life. There are, of course, the customary observations on vineyards and manufacture of wines, but the only remarks of particular interest to us are the following. Cologne, at that time a sovereign city of about 60,000 inhabitants and having no territory outside its walls, was the most northern spot on earth where wine was made. Their first grapes had originally come from Orleans, but since then others had been brought from Alsace and Champagne. Jefferson also informs us that it was only 32 years since the first vine had been sent from Cassel, near Mayence, to the Cape of Good Hope, where Cape wine was made as a consequence. The Cape, Jefferson supposed, was the most southern spot on

³⁹ (13, XVII, 214.)

⁴⁰ *Trifolium incarnatum*.

⁴¹ Furze = whin, *Ulex europaeus*.

earth where wine was made, and he regarded it as singular that the same vine should have furnished two wines as much opposed to each other in quality as they were apart in location.

In Heidelberg, apple, pear, cherry, peach, apricot, and almond were all in bloom (April 14), and at the village of Kaeferthal was a plantation of rhubarb, started in 1769, which supplied the apothecaries of Frankfort and England.

INTRODUCTION OF NEW CROP PLANTS INTO AMERICA

As a result of his long sojourn in France and especially of his having seen so much of the agricultural activities there, Jefferson became imbued with the idea that certain crop plants of Europe, theretofore not cultivated in the States, should be introduced into America. His enthusiasm in this direction became so great and so enduring that years later in an appendix to his autobiography, begun in 1821 at the age of 77, he concluded with the very strong statement that

"The greatest service which can be rendered any country is, to add an useful plant to its culture; especially, a bread grain; next in value to bread is oil."⁴²

On an earlier occasion, when thanking someone for some seeds of the breadfruit tree to be introduced into the southern States, he concluded with the remark that

"One service of this kind rendered to a nation, is worth more to them than all the victories of the most splendid pages of their history, and becomes a source of exalted pleasure to those who have been instrumental to it. May that pleasure be yours, and your name be pronounced with gratitude by those who will at some future time be tasting the sweets of the blessings you are now procuring them."⁴³

What he advocated, he practiced himself, and scarcely left a stone unturned which held any promise of adding to the vegetative richness of his homeland. We have already observed in our consideration of his farming activities that he imported legumes from abroad to restore fertility to his soil, and our attention now becomes directed to a variety of other plants.

In 1786, while still in Paris, Jefferson had occasion to acknowledge election to membership in the South Carolina Agricultural Society which had been organized the previous year and with which he thereafter carried on considerable correspondence. In reciprocation for the honor thus accorded him, he expressed the hope of being able to render some service

"by forwarding to the society such new objects of culture, as may be likely to succeed in the soil and climate of South Carolina. In an infant country,

⁴² (13, I, 259.)

⁴³ Letter to Mr. Giroud, May 22, 1797 (13, IX, 387).

as ours is, these experiments are important. We are probably far from possessing, as yet, all the articles of culture for which nature has fitted our country. To find out these, will require abundance of unsuccessful experiments. But if, in a multitude of these, we make one useful acquisition, it repays our trouble. Perhaps it is the peculiar duty of associated bodies, to undertake these experiments. Under this sense of the views of the society, and with so little opportunity of being otherwise useful to them, I shall be attentive to procure for them the seeds of such plants, as they will be so good as to point out to me, or as shall occur to myself as worthy of their notice. I send at present, by Mr. McQueen, some seeds of a grass, found very useful in the southern parts of Europe, and particularly, and almost solely cultivated in Malta. It is called by the names of Sulla, and Spanish St. Foin, and is the *Hedysarum coronarium*⁴⁴ of Linnaeus. It is usually sown early in autumn. I shall receive a supply of fresher seed, this fall, which I will also do myself the honor of forwarding to you. I expect, in the same season, from the south of France, some acorns of the cork oak, which I propose for your society, as I am persuaded they will succeed with you. I observed it to grow in England, without shelter; not well, indeed, but so as to give hopes that it would do well with you."⁴⁵

Two years later Jefferson was promising more seed of the Spanish St. Foin, some of which he had received by then direct from Malta.⁴⁶ He fulfilled his promise, but the shipment apparently was lost at sea, for years later he bemoaned this failure.⁴⁷ In the same letter we learn also of similar disappointment in regard to the other plant mentioned in the above quoted correspondence:

"I have been long endeavoring to procure the Cork tree from Europe, but without success. A plant which I brought with me from Paris died after languishing some time, and of several parcels of acorns received from a correspondent at Marseilles, not one ever vegetated. I shall continue my endeavors, although disheartened by the nonbalance of our Southern fellow citizens, with whom alone they can thrive."⁴⁸

In 1808 Jefferson received

"a bottle of the oil of Beni,⁴⁹ believed to be a sesamum. I did not believe there existed so perfect a substitute for olive oil. Like that of Florence, it has no taste, and is perhaps more limpid. A bushel of seeds yields three gallons of oil; and Governor Milledge, of Georgia, says the plant will grow wherever the Palm Christi will. It is worth your attention, and you can probably get seed from Colonel Fen."⁵⁰

⁴⁴ This European herb, valued as forage, is sometimes cultivated for its pink flowers as French honeysuckle.

⁴⁵ Letter to William Drayton, May 6, 1786 (13, V, 311).

⁴⁶ Letter to William Drayton, January 13, 1788 (13, VI, 413).

⁴⁷ Letter to James Ronaldson, January 12, 1813 (13, XIII, 204).

⁴⁸ Sesame or Benne oil, from *Sesamum indicum*, is one of the staple food oils of India, and has limited use in salads, soaps and pharmaceuticals.

⁴⁹ Letter to R. R. Livingston, January 3, 1808 (13, XI, 417).

Three days later he wrote to another correspondent and informs us that

"The African Negroes brought over to Georgia a seed which they called *beni*, and the botanists *sesamum*. I lately received a bottle of the oil, which was eaten with salad by various companies. All agree it is equal to the olive oil. A bushel of seeds yields three gallons of oil. I propose to cultivate it for my own use at least."⁵⁰

In this same letter Jefferson called attention to a report in the transactions of the Agricultural Society of Paris that they were cultivating Jerusalem artichoke for animal feed, 10,000 pounds to the acre, which they said was three times as much as they generally made of potatoes. His efforts with the *beni* seeds were not very successful:

"I sowed some of the *Benni* seed the last year, and distributed some among my neighbors; but the whole was killed by the September frost. I got a little again the last winter, but it was sowed before I received your letter. Colonel Fen of New York receives quantities of it from Georgia, from whom you may probably get some through the Mayor of New York. But I little expect it can succeed. It is about as hardy as the cotton plant, from which you may judge of the probability of raising it at Hudson."⁵¹

Culture of the almond tree, Jefferson wrote from France, was so precarious that no one but persons of capital could depend on it for subsistence,⁵² and the fig and mulberry were so well known in America that nothing needed to be said about them. Since the latter two were cared for in France by women and children, Jefferson looked upon them, in contemplating conditions in America, as

"earnestly to be desired in countries where there are slaves."⁵³

Capers also attracted Jefferson's attention in Europe, and in 1792 he imported some from Marseille. He sent them to Charleston⁵⁴ for trial there and expressed the opinion that they would probably succeed in America, that their culture would offer a very great and immediate profit.⁵⁵ He also wrote:

"The caper, though a more tender plant, is more certain in its produce, because a mound of earth of the size of a cucumber hill, thrown over the plant in the fall, protects it effectually against the cold of winter. When the danger of frost is over in the spring, they uncover it, and begin its culture. There is a great deal of this in the neighborhood of Toulon. The plants are set about eight feet apart, and yield, one year with another, about two pounds of caper each, worth on the spot sixpence sterling per pound. They require little culture, and this may be performed either with the plough or hoe. The principal work is the gathering of the fruit as it forms. Every plant must be

⁵⁰ Letter to John Taylor, January 6, 1808 (13, XI, 113).

⁵¹ Letter to Horatio G. Spafford, May 14, 1809 (13, XII, 278).

⁵² Letter to William Drayton, July 30, 1787 (13, VI, 193).

⁵³ Letter to George Washington, May 16, 1792 (13, VII, 337).

⁵⁴ Letter to Edward Rutledge, July 14, 1787 (13, VI, 169).

picked every other day, from the last of June till the middle of October. But this is the work of women and children. This plant does well in any kind of soil which is dry, or even in walls where there is no soil, and it lasts the life of a man. Toulon would be the proper port to apply for them. I must observe, that the preceding details cannot be relied on with the fullest certainty, because, in the canton where this plant is cultivated, the inhabitants speak no written language, but a medley, which I could understand but very imperfectly."⁵⁵

The foregoing economic plants, while interesting in having appealed to Jefferson, were really secondary in his considerations. For the important items we must refer to the quotation on page 585 at the beginning of this chapter. That sentence was part of one of eleven paragraphs constituting what Jefferson called "Note G" in the Appendix to his autobiography, those eleven paragraphs being devoted to that number of items of his accomplishments, in an attempt to answer the question in his own mind whether his country was any better for his having lived. This note, apparently, was never completed. It briefly mentioned disestablishment of a State church, abolition of entails and prohibition of slave importation, and the greatest of all was only named, "The Declaration of Independence." The Lewis and Clark Expedition was not even mentioned, though Jefferson's successful promotion of that project, as we shall later note, was his foremost contribution to science; it undoubtedly would have been included had that note ever been completed. It is because of this omission that we find particular significance in his having included, so far as he did formulate that note, the following two paragraphs:

"In 1789 and 1790, I had a great number of olive plants, of the best kind, sent from Marseilles to Charleston, for South Carolina and Georgia. They were planted, and are flourishing; and, though not yet multiplied, they will be the germ of that cultivation in those States.

In 1790, I got a cask of heavy upland rice, from the river Denbigh, in Africa, about lat. 9° 30' North, which I sent to Charleston, in hopes it might supersede the culture of the wet rice, which renders South Carolina and Georgia so pestilential through the summer. It was divided, and a part sent to Georgia. I know not whether it has been attended to in South Carolina; but it has spread in the upper parts of Georgia, so as to have become almost general, and is highly prized. Perhaps it may answer in Tennessee and Kentucky."⁵⁶

Because of the importance which Jefferson thus attached to these two incidents, so briefly mentioned in the closing years of his life, it is most appropriate that we carefully examine all his previous correspondence which may shed any light on the two topics. From them we acquire the following picture.

⁵⁵ Letter to William Drayton, July 30, 1787 (13, VI, 193).

⁵⁶ (13, I, 258.)

Rice.⁵⁷ While in France as American Minister to that country, Jefferson observed that the annual consumption of rice, particularly in Paris, was considerable, amounting to about 82,000 quintals (quintal = 220 pounds), and he regarded it as his duty to determine what the sources of supply were, to what extent the material was imported from America, where it had been in cultivation since the latter part of the sixteenth century, and whether the American proportion of that supply could not be increased. Difficulties were encountered in his attempts to secure accurate information on these matters from retailers of rice, but his persistent inquiries finally produced the following information.

The dealers in France were in the habit of selling two qualities of rice, one from Carolina with which they were supplied chiefly from England; the other known as Piedmont rice from Italy. The Carolina rice was long, slender, attractively white, and served well when prepared *au lait*, that is, with milk and sugar, but not so well when prepared in a fashion known as *au gras*. That of Piedmont was shorter, thicker and less white, but was the better when served *au gras*. It was preferred, therefore, to the American rice, though the more pleasing appearance of the latter resulted in its imports from America being approximately equal to those from Piedmont.

The difference in quality between the two kinds, accounting for the preference exhibited toward that from Piedmont, was attributed by the rice dealers to a difference in techniques between the American and French methods of preparing the material for market. The Carolina rice, they figured, was husked with a type of machine that broke it more than did the French instrument, and less care was observed in separating the broken from the unbroken grains. The Carolina rice was less expensive to the dealers than that of Piedmont, but since they were obliged to sort the whole grains from the broken, in order to satisfy the taste of their customers, the dealers had to charge as much for the first quality Carolina rice, when sorted, as for that of Piedmont. Second and third qualities, obtained by sorting, sold much cheaper.

Mechanically inclined as Jefferson was, among his many accomplishments, he determined to learn in what way the machines of Piedmont differed from those of South Carolina and why they supplied the European market

⁵⁷ Account gathered from letters to (all in citation No. 13):

John Jay, January 2, 1786 (VII, 28); May 4, 1787 (VI, 111).

Edward Rutledge, July 14, 1787 (VI, 169); July 18, 1788 (VII, 79); September 18, 1789 (VII, 463).

Dr. David Ramsay, October 27, 1786 (V, 455).

John Adams, July 1, 1787 (VI, 146).

James Maury, November 13, 1787 (VI, 374).

George Washington, December 4, 1788 (VII, 223).

Benjamin Vaughan, May 17, 1787 (VII, 359); June 27, 1790 (VIII, 49).

Ralph Izard, August 1, 1787 (VI, 209).

with rice which was less broken than that from America. It was in connection with his journey into southern France in 1787 that an opportunity presented itself for acquiring this information. Frustrated at first in his attempt to learn the answer in Marseille, which was the great emporium of the Levant and of Italy, he set out that year on a three-weeks journey across the Alps into the rice country of Italy between Vercelli and Pavia. There he visited the rice fields of the Venellese and Milanese, saw their machines in operation, and found them almost identical with those of Carolina. He thereupon concluded that the Italian rice which, incidentally, came from Lombardy and not Piedmont as incorrectly implied in its common name, was of a species different in form, color and quality from that of Carolina. He founded this conclusion partly on the reports of a certain M. Poivre, a former Governor of the Isle of France, who had travelled through several countries of Asia, observing in particular the agriculture of those lands. He had written upon rice and reported six kinds as being cultivated in Cochin China, three of them requiring water and three being of the upland type, growing on highlands. According to Poivre, Carolina rice was of the "white" variety, different from these, and Jefferson understood, as we know today, that it had originally come from Madagascar. The effect of time, culture, and climate, Jefferson thought, may have accentuated any original differences between the Carolina and Lombardy strains.

It is only natural that Jefferson should have then become interested in the prospects of getting some of the unhusked rice of Piedmont or Lombardy, as one may prefer to call it, to America in order that its cultivation here might be undertaken. But the government of Turin, in the vicinity of which the finest strains were grown, prohibited its export in that form on pain of death. To circumvent this restriction, Jefferson resorted to a little smuggling activity by engaging a muleteer to run a couple of sacks across the Apennines to Genoa, beyond which their further transit would not have been so precarious.⁵⁸ Jefferson was skeptical of the success of this venture and so he filled his coat and surtout pockets with a few pounds of the best kind he could obtain from Vercelli. These he sent to William Drayton of the agricultural society in South Carolina, not in one package but in three parcels by as many different ways to be assured of their delivery. The fate of the shipment entrusted to the mule is not revealed in any of Jefferson's letters, but the other three bundles from Turin, we know, arrived safely in Charleston. Their contents were distributed among the rice growers of the South, ten and twelve grains to each of several planters.

Jefferson was not satisfied, however, merely with this smuggling exploit. He continued his investigations and the next year he informed Dr. Drayton

⁵⁸ In his own words: "Poggio, a muleteer, who passes every week between Vercelli and Genoa, will smuggle a sack of rough rice for me to Genoa; it being death to export it in that form" (13, XVII, 192).

that another kind of rice obtainable from the Levant was considered by some not only to be different in quality from that of Piedmont but even as superior to it. He sent a quantity of this strain in the husked form to Dr. Drayton, and took measures to obtain unhusked grains of it for him. In reference to the American and Old World varieties he then continued :

"I should think it certainly advantageous to cultivate, in Carolina and Georgia, the two qualities demanded at market; because the progress of culture, with us, may soon get beyond the demand for the white rice; and because too, there is often a brisk demand for the one quality, when the market is glutted with the other. I should hope there would be no danger of losing the species of white rice, by a confusion with the other. This would be a real misfortune, as I should not hesitate to pronounce the white, upon the whole, the most precious of the two, for us. The dry rice of Cochin-China has the reputation of being the whitest to the eye, best flavored to the taste, and most productive. It seems then to unite the good qualities of both the others known to us. Could it supplant them, it would be a great happiness, as it would enable us to get rid of those ponds of stagnant water, so fatal to human health and life. But such is the force of habit, and caprice of taste, that we could not be sure beforehand it would produce this effect. The experiment, however, is worth trying, should it only end in producing a third quality, and increasing the demand. I will endeavor to procure some to be brought from Cochin-China. The event, however, will be uncertain and distant."⁵⁹

Six months later he sent some rough rice for experimental purposes from Egypt, and remarked that the young Prince of Cochin China, who had recently left Paris and with whom Jefferson had presumably become acquainted, promised to send him some dry rice from that country.⁶⁰ It is from a letter of 20 years later, however, that we learn of his final success in introducing into the States a type of upland rice from the River Denbigh in Africa :

"In answer to the inquiries of the benevolent Dr. De Carro on the subject of the upland or mountain rice, *Oryza Mutica*, I will state to you what I know of it. I first became informed of the existence of a rice which would grow in uplands without any more water than the common rains, by reading a book of Mr. De Poivre, who had been Governor of the Isle of France, who mentions it as growing there and all along the coast of Africa successfully, and as having been introduced from Cochin-China. I was at that time (1784-89) in France, and there happened to be there a Prince of Cochin-China, on his travels, and then returning home, I obtained his promise to send me some. I never received it however, and mention it only as it may have been sent, and furnished the grounds for the inquiries of Dr. De Carro, respecting my receiving it from China. When at Havre on my return from France, I found there Captain Nathaniel Cutting, who was the ensuing spring to go on a voyage along the coast of Africa. I engaged him to inquire for this; he was there just after the harvest, procured and sent me a thirty-gallon

⁵⁹ Letter to William Drayton, July 30, 1787 (13, VI, 193).

⁶⁰ Letter to William Drayton, January 13, 1788 (13, VI, 413).

cask of it. It arrived in time the ensuing spring to be sown. I divided it between the Agricultural Society of Charleston and some private gentlemen of Georgia, recommending it to their care, in the hope which had induced me to endeavor to obtain it, that if it answered as well as the swamp rice, it might rid them of that source of their summer diseases. Nothing came of the trials in South Carolina, but being carried into the upper hilly parts of Georgia, it succeeded there perfectly, has spread over the country, and is now commonly cultivated; still, however, for family use chiefly, as they cannot make it for sale in competition with the rice of the swamps. The former part of these details is written from memory, the papers being at Monticello which would enable me to particularize exactly the dates of times and places. The latter part is from the late Mr. Baldwin, one of those whom I engaged in the distribution of the seed in Georgia, and who in his annual attendance on Congress, gave me from time to time the history of its progress. It has got from Georgia into Kentucky, where it is cultivated by many individuals for family use. I cultivated it two or three years at Monticello, and had good crops, as did my neighbors, but not having conveniences for husking it, we declined it. I tried some of it in a pot, while I lived in Philadelphia, and gave seed to Mr. Bartram. It produced luxuriant plants with us both, but no seed; nor do I believe it will ripen in the United States as far north as Philadelphia."⁶¹

In Jefferson's correspondence regarding rice there is an incidental though interesting reference to the famous Captain Bligh of Bounty fame. Captain Bligh, in charge of the ship *Bounty*, had been sent to the South Sea islands to stock breadfruit trees for transplanting into the British West Indies. His allegedly tyrannous management of the crew led to mutiny near the Friendly Islands, and Bligh, with 19 of his men, were set adrift in an open boat. In June, 1789, they landed on the island of Timor, and eventually made their way back to England. Bligh was subsequently commissioned to repeat the voyage and this time succeeded in his commission. The relationship of all this to Jefferson is revealed in a letter to him in 1790 from Jamaica, from one Samuel Vaughan.⁶² From it we gather that Jefferson had asked Vaughan's father for some seeds of mountain rice, the request had been transmitted to the son, and the son was replying to the effect that he could not comply but instead was sending 40 seeds, twenty with the letter and twenty otherwise, of a variety of rice that was plentiful in the central parts of Hispaniola. The point is somewhat ambiguous in his letter, but it was probably with reference to this same rice, that Vaughan wrote that the seeds which he had, had been brought from Timor by Captain Bligh. The implication is that Bligh, despite his predicament, brought seed rice with him, and that within a year's time it was abundant in Hispaniola, all of which seems rather unlikely. Nevertheless, Jefferson believed in this origin of the rice, for five months earlier we find him acknowledging receipt

⁶¹ Letter to Dr. Benjamin Waterhouse, December 1, 1808 (13, XII, 204).

⁶² Letter from Samuel Vaughan, Jr., October 4, 1790 (15, 44).

of some dry rice from the Moluccas, and informing Benjamin Vaughan⁶³ that some of the seed had been sent to Virginia; the others had been sowed in pots, and at the time of his writing he had 23 young plants, but feared that there was not enough of summer remaining for them to mature.

Despite Jefferson's enthusiasm in the matter, and the assertions of certain biographers that his introduction of dry rice brought prosperity and wealth to parts of the South, we must note that cultivation of upland rice in the United States never became significant.

Olives.⁶⁴ Jefferson's interest in olive trees as a crop plant for America was scarcely less intense than that in rice, and his enthusiastic advocacy of their cultivation in the States is well displayed in a letter to Dr. Drayton from Paris in 1787:

"The olive is a tree the least known in America, and yet the most worthy of being known. Of all the gifts of heaven to man, it is next to the most precious, if it be not the most precious. Perhaps it may claim a preference even to bread, because there is such an infinitude of vegetables which it renders a proper and comfortable nourishment. In passing the Alps at the Col de Tende, where they are mere masses of rock, wherever there happens to be a little soil, there are a number of olive trees, and a village supported by them. Take away these trees, and the same ground in corn would not support a single family. A pound of oil, which can be bought for three or four pence sterling, is equivalent to many pounds of flesh, by the quantity of vegetables it will prepare, and render fit and comfortable food. Without this tree, the country of Provence and territory of Genoa would not support one-half, perhaps not one-third, their present inhabitants. The nature of the soil is of little consequence if it be dry. The trees are planted from fifteen to twenty feet apart, and when tolerably good, will yield fifteen or twenty pounds of oil yearly, one with another. There are trees which yield much more. They begin to render good crops at twenty years old, and last till killed by cold, which happens at some time or other, even in their best positions in France. But they put out again from their roots. In Italy, I am told, they have trees two hundred years old. They afford an easy but constant employment through the year, and require so little nourishment, that if the soil be fit for any other production, it may be cultivated among the olive trees without injuring them. The northern limits of this tree are the mountains of the Cevennes, from about the meridian of Carcassonne to

⁶³ Letter to Benjamin Vaughan, June 27, 1790 (13, VIII, 49).

⁶⁴ Account founded on letters to (all in citation No. 13):

The President of the United States, May 1, 1791 (VIII, 189), May 16, 1792 (VIII, 337).
C. C. Pinckney, October 8, 1792 (VIII, 412).

Edward Rutledge, July 14, 1787 (VI, 169), November 19, 1788 (VII, 50), September 18, 1789 (VII, 463).

Wm. Drayton, July 30, 1787 (VI, 193).

George Wythe, September 16, 1787 (VI, 296).

M. de Bertrous, February 21, 1788 (VI, 431).

James Ronaldson, January 12, 1813 (XIII, 204).

Stephan Catalan, December 2, 1792 (XIX, 98).

the Rhone, and from thence, the Alps and Apennines as far as Genoa, I know and how much farther I am not informed. The shelter of these mountains may be considered as equivalent to a degree and a half of latitude, at least, because westward of the commencement of the Cevennes, there are no olive trees in $43\frac{1}{2}^{\circ}$ or even 43° of latitude, whereas, we find them *now* on the Rhone at Pierrelatte, in $44\frac{1}{2}^{\circ}$, and *formerly* they were at Tains, above the mouth of the Isere, in 54° , sheltered by the near approach of the Cevennes and Alps, which only leave there a passage for the Rhone. Whether such a shelter exists or not in the States of South Carolina and Georgia, I know not. But this we may say, either that it exists or that it is not necessary there, because we know that they produce the orange in open air; and wherever the orange will stand at all, experience shows that the olive will stand well, being a hardier tree. Notwithstanding the great quantities of oil made in France, they have not enough for their own consumption, and, therefore, import from other countries. This is an article, the consumption of which will always keep pace with its production. Raise it, and it begets its own demand."

"Little is carried to America, because Europe has it not to spare. We, therefore, have not learned the use of it. But cover the southern states with it, and every man will become a consumer of oil, within whose reach it can be brought in point of price. If the memory of those persons is held in great respect in South Carolina who introduced there the culture of rice, a plant which sows life and death with almost equal hand, what obligations would be due to him who should introduce the olive tree, and set the example of its culture. Were the owner of slaves to view it only as the means of bettering their condition, how much would he better that by planting one of those trees for every slave he possessed. Having been myself an eye witness to the blessings which this tree sheds on the poor, I never had my wishes so kindled for the introduction of any article of new culture into our own country. South Carolina and Georgia appear to me to be the States, wherein its success, in favorable positions at least, could not be doubted, and I flattered myself it would come within the views of the society for agriculture to begin the experiments which are to prove its practicability. Carcassonne is the place from which the plants may be most certainly and cheaply obtained. They can be sent from thence by water to Bordeaux, where they may be embarked on vessels bound for Charleston. There is too little intercourse between Charleston and Marseilles to propose this as the port of exportation. I offer my services to the society for the obtaining and forwarding any number of plants which may be desired."

A year later in advising Edward Rutledge concerning things to be noted by the latter during his travels through France, Jefferson was still interested in determining the northern limit of culture of the trees in that country:

"I must press on you, my dear Sir, a very particular attention to the climate and culture of the olive tree. This is the most interesting plant in existence for South Carolina and Georgia. You will see in various places that it gives being to whole villages in places where there is not soil enough to subsist a family by the means of any other culture. But consider it as the means of bettering the condition of your slaves in South Carolina. See in the poorer parts of France and Italy what a number of vegetables are rendered eatable by the aid of a little oil, which would otherwise be useless.

Remark very particularly the northern limits of this tree, and whether it exists by the help of shelter from the mountains, etc. I know this is the case in France. I wish to know where the northern limit of this plant crosses the Apennines; where it crosses the Adriatic and the Archipelago, and if possible what course it takes through Asia."

Jefferson's recommendations, as we might expect, were not without effect, and in another letter from Paris, thanking M. de Bertrous for a book on olive culture which he had just sent to Jefferson, we read:

"This is a precious present to me, and I pray you to accept my thanks for it. I am just gratified by letters from South Carolina, which inform me that in consequence of the information I had given them on the subject of the olive tree, and the probability of its succeeding with them, several rich individuals propose to begin its culture there. It will not interfere with the commerce of France, because she imports much more oil than she exports, and because the consumption of oil in the United States at present, is so inconsiderable, that should their demand be totally withdrawn at the European market, and supplied at home, it will produce no sensible effect in Europe. We can never produce that article in very great quantity, because it happens that in our two southernmost States, where only the climate is adapted to the olive, the soil is so generally rich as to be unfit for that tree, and proper for other productions of more immediate profit."

In two letters of 1792 we learn that the Agricultural Society of South Carolina had also followed Jefferson's advice to the extent of employing someone in Marseille to raise and send them olive trees, and that 40 olive tree cuttings had arrived from there at Baltimore, as well as a box of seeds. The former were to be grafted on stock raised from the seed. Another cargo was on its way from Bordeaux. A year later there were in Charleston 100 olive trees which had resulted from Jefferson's instrumentality, and another 100 had arrived in Philadelphia from Marseille, which also he was sending to Charleston.

It is regrettable, in view of all his good intentions, that Jefferson's devotion to introducing olive trees into America was not at all so successful as was his promotion of rice. This we learn from a letter of his in 1813 in which he bemoaned the fact that 25 years had elapsed since he sent two shipments of about 500 plants from Aix, the finest olives in the world, and that if any of them still existed it was merely as curiosities in the gardens of some Southern fellow citizens. Not a single orchard of them had been planted.

INTRODUCTION OF AGRICULTURAL CROPS FROM AMERICA INTO EUROPE

Jefferson's interest in the introduction of food plants was not limited to bringing such sources to America. He saw also the possibility of the acquisition by Europe of valuable plants from America, and various passages in his correspondence testify to this concern. On one occasion, for instance, when a French author sent him a treatise on the culture of sugar cane and cotton in France, Jefferson replied:

"The introduction of new cultures, and especially of objects of leading importance to our comfort, is certainly worthy the attention of every government, and nothing short of actual experiment should discourage an essay of which any hope can be entertained. Till that is made, the result is open to conjecture; and I should certainly conjecture that the sugar cane could never become an article of profitable culture in France. We have within the ancient limits of the United States, a great extent of country which brings the orange to advantage, but not a foot in which the sugar cane can be matured. France, within its former limits, has but two small spots, (Olioules and Hières) which brings the orange in open air, and *a fortiori*, therefore, none proper for the cane. I should think the sugar maple more worthy of experiment. There is no part of France of which the climate would not admit this tree. I have never seen a reason why every farmer should not have a sugar orchard, as well as an apple orchard. The supply of sugar for his family would require as little ground, and the process of making it as easy as that of cider. Mr. Micheaux, your botanist here, could send you plants as well as seeds, in any quantity from the United States. I have no doubt the cotton plant will succeed in some of the southern parts of France. Whether its culture will be as advantageous as those they are now engaged in remains to be tried."

After some remarks upon the economics of wine production in America, Jefferson continued:

"In general, it is a truth that if every nation will employ itself in what is fittest to produce, a greater quantity will be raised of the things contributing to human happiness, than if every nation attempts to raise everything it wants within itself. The limits within which the cotton plant is worth cultivating in the United States, are the Rappahannock river to the north, and the first mountains to the west. And even from the Rappahannock to the Roanoke, we only cultivate for family use, as it cannot there be afforded at market in competition with that of the more Southern region. The Mississippi country, also within the same latitudes, admits the culture of cotton."⁶⁵

On several other occasions, too, Jefferson was instrumental in at least attempting to get American plants into France. We do not know whether he was always successful, however, for his correspondence does not tell, and hostilities between France and England at the time made shipping very precarious. While residing in Paris, for instance, he sent for some

"seeds of the *Dionaea Muscipula*, or Venus fly-trap, called also with you, I believe, the Sensitive Plant."⁶⁶

and at another time he asked someone to procure for him two or three hundred "paccan" nuts from the "western country," suggesting that they be obtained at Pittsburgh and giving directions for sending them in a box of sand.⁶⁷ His correspondent could not have been well acquainted with what Jefferson wanted, for later the same year we find him explaining that

⁶⁵ Letter to M. Lasteyrie, July 15, 1808 (13, XII, 90).

⁶⁶ Letter to Mr. Hawkins, August 13, 1786 (13, V, 390).

⁶⁷ Letter to Mr. Hopkinson, January 3, 1786 (13, V, 243).

"The paccan-nut is, as you conjecture, the Illinois nut. The former is the vulgar name south of the Potomac, as also with the Indians and Spaniards, and enters also into the Botanical name which is *Juglans Paccan*."⁶⁸

It would seem safe to assume that Jefferson made similar efforts to fill the request of another correspondent who had sent him from London the kinds of peas and vetch cultivated in England and which Jefferson wanted for his own farm. This writer asked that he be sent seed of the Buffalo clover, *Trifolium reflexum*, which was said to abound west of the mountains; also of some shrub which he could not name but which the famous John Bartram had mentioned to him as growing wild only in Jefferson's neighborhood, the fruit of which produced a pure oil.⁶⁹

Elsewhere Jefferson tells of having furnished cotton seed from our southern States to the Agricultural Society of Paris upon their request for experimental purposes, and two or three barrels of Virginia May wheat to the London Board of Agriculture. Washington, he relates, received seed of perennial succory from the same French society, and he himself received from another member of it, seed of the famous Swedish turnip. Jefferson told of these exchanges in illustrating how well agricultural societies functioned with mutual respect despite the wars between their respective countries.⁷⁰

International trade in plant products also received consideration. In discussing such commerce with Portugal, Jefferson expressed the opinion to John Adams that flour could be sold to that country for less than wheat because in shipping the latter, the bran, which did not pay its own freight, also had to be carried, and much was lost in transit because of weevils and heat in the holds of vessels. With further reference to trade in plant products with Portugal, he continued:

"Coffee. Can they not furnish us with this article from Brazil?

Sugar. The Brazil sugars are esteemed, with us, more than any other.

Chocolate. This article, when ready made, as also the cocoa, becomes so soon rancid, and the difficulties of getting in fresh have been so great in America, that its use has spread but little. The way to increase its consumption would be, to permit it to be brought to us immediately from the country of its growth. By getting it good in quality, and cheap in price, the superiority of the article, both for health and nourishment, will soon give it the same preference over tea and coffee in America, which it has in Spain, where they can get it by a single voyage, of course, while it is sweet. The use of the sugars, coffee, and cotton of Brazil, would also be much extended by a similar indulgence.

Ginger and spices from the Brazils, if they had the advantage of a direct transportation, might take the place of the same articles from the East Indies.

⁶⁸ Letter to Mr. Hopkinson, December 23, 1786 (13, VI, 21).

⁶⁹ Letter from Wm. Strickland, May 28, 1796 (15, 61).

⁷⁰ Letter to John Hollins, February 19, 1809 (13, XII, 252).

Ginseng. We can furnish them with enough to supply their whole demand for the East Indies."⁷¹

RESUMÉ

In any attempt to evaluate Jefferson's position in the history of American agriculture, one must take into consideration the pioneering aspects of his husbandry and their influence on his contemporaries, rather than look for any outstanding yields in the crops which he produced. He was among the first in the New World to initiate the elevation of farming to a science, to experiment with new crops and new techniques, and to keep records of his activities. Rotation of crops as a means of preserving soil fertility was scarcely known in America before he and a few other enterprising farmers of the day adopted it as a fundamental element in their husbandry. It is because of these innovations as well as others, not at all discussed in this study, such as his introduction of Merino sheep and his construction of a prize-winning mold-board, that among the praises written of him in his relation to agriculture, we find that "he did more for its promotion than any other statesman that ever lived, and deserves to be the perpetual Emeritus President of the Patrons of Husbandry," and that if he "had done nothing else save to aid man's knowledge of agriculture, he would have been a benefactor."

(The second and third parts of this study as well as the bibliography will appear in later issues of the BULLETIN.)

THE NEW YORK BOTANICAL GARDEN
NEW YORK

⁷¹ Letter to John Adams, November 27, 1785 (13, V, 222).

THE MORPHOLOGY OF *SPHAEROSTILBE AURANTIICOLA*
(B. & BR.) PETCH^{1, 2, 3}

E. S. LUTTRELL

Sphaerostilbe aurantiicola belongs among the Hypocreales. It was described as *Nectria aurantiicola* in 1873 by Berkeley and Broome from material collected in Ceylon on scale insects parasitizing orange twigs. In 1921 Petch (22) transferred it to the genus *Sphaerostilbe*. Although the name *Nectria aurantiicola* is antedated by *Sphaerostilbe coccophila*, which was applied to the perithecial stage by the Tulasnes in 1861, the latter name was discarded by Petch. The Tulasnes had based their description upon perithecial material from Italy and connected it with the conidial form *Microcera coccophila* which Desmazières had described in 1848 from a collection on scale insects in France. Petch found, however, that perithecia were present in the specimens upon which Desmazières had based *Microcera coccophila* and that they belonged to *Sphaerostilbe flammea* Tul. *Sphaerostilbe coccophila* was, therefore, a composite species consisting of the conidial stage of one species and the perithecial stage of another. In order to avoid confusion Petch selected *Sphaerostilbe aurantiicola* as the correct name. This is, perhaps, a doubtful basis for the rejection of the name first applied to the perithecial stage of the fungus, but since Petch's usage appears to have gained acceptance, it is employed herein.

Sphaerostilbe aurantiicola occurs throughout the world as a parasite upon various species of scale insects. Petch (22) examined collections of it from France, Italy, Madagascar, Ceylon, India, Formosa, Japan, Dominica, and the United States. In Florida alone it has been reported (Watson and Berger 28) upon thirteen species of scale insects.

It is of importance in the biological control of scale insects—especially the San Jose scale—on fruit trees in Florida. Its importance in this respect was first recognized by Rolfs (23) in 1897. In certain Florida orchards on some trees which previously had been severely infested with San Jose

¹ Paper No. 124, Journal Series, Georgia Agricultural Experiment Station.

² Specimens of the fungus, collection No. 5002, and slides representative of the series upon which this study was based have been deposited in the Farlow Herbarium, Harvard University. A culture, No. 76, has been deposited in the American Type Culture Collection, Georgetown University School of Medicine.

³ I am indebted to Dr. B. B. Higgins, Georgia Agricultural Experiment Station, Dr. B. O. Dodge, New York Botanical Garden, and Dr. F. A. Wolf, Duke University, for examining the preparations and criticizing the manuscript and to Mr. J. Gordon Futral of this Station for his advice and assistance in taking the photomicrographs reproduced in figs. 1-13.

scale, he found that the scale had been almost entirely eliminated by *Sphaerostilbe aurantiicola*. He recommended the introduction of the fungus into orchards in which it was not already present by tying branches bearing diseased scales to the infested trees or by spraying the trees with a suspension of conidia from nature or from cultures. This method of natural control of the San Jose scale has been successful in Florida because climatic conditions there favor the development of the fungus (Watson and Berger 28); elsewhere it has not been of much consequence. Smith (24) obtained the fungus from Rolfs and introduced it into New Jersey where it spread but proved to be a failure in control of the scale. Earle (8) reported that in Alabama, because of the dry climate, the fungus was not active enough to control scale efficiently. Forbes (10) early stated that it gave promise of being effective in the control of the San Jose scale in Illinois, but in later reports he made no mention of it.

Although no attempt has been made to utilize the fungus in the control of scale insects in Georgia, in the vicinity of the Georgia Agricultural Experiment Station it is commonly present on obscure scale [*Chrysomphalus obscurus* (Comst.)] on water oak (*Quercus nigra* L.). Since it was available in all stages of development, a special morphological study of it was made. The present report is concerned primarily with the development of the perithecium of *Sphaerostilbe aurantiicola* and a comparative review of the published accounts of perithecial development in other species of Hypocreales. Accounts of the taxonomy, gross morphology, and biology of this fungus may be found in papers by Petch (22) and Rolfs (23).

METHODS

Infected scales were stripped from the bark or else a thin layer of bark bearing the scale was shaved from the infested branch. The fixative employed was Formalin-propionic-alcohol solution (70 % ethyl alcohol, 90 parts; propionic acid, 5 parts; Formalin, 5 parts). The fixed material was washed in 70 per cent alcohol, passed through a graduated series of tertiary butyl alcohols, and embedded in 60 degree Tissuemat. Serial sections were cut at a thickness of 8 microns. The sections were treated with 1 per cent chromic acid, stained in a fresh solution of Haidenhain's haematoxylin, differentiated with a saturated solution of picric acid, and mounted in balsam. Some were counter-stained with fast green dissolved in clove oil, but these were not superior to sections stained with haematoxylin only. In addition, freehand sections and smears of fresh and fixed material mounted in water or in lactophenol containing 1 per cent cotton blue were studied. Drawings were made with the aid of an Abbe camera lucida. Photomicrographs were taken with a Leitz Makam photomicrographic apparatus on medium lantern slide plates.

THE CONIDIAL STAGE

The first macroscopic sign of infection of the scale insect is the appearance of conidial fructifications. These are abundant throughout the year but are most conspicuous during periods of rainy weather in spring or in late fall. The fructifications are 0.5–1.5 mm. high. They may be stilboid in form, consisting of a short, whitish stalk surmounted by a broader, globular, orange conidial head. (Generally, however, the stalk is poorly developed, the head being almost sessile (fig. 2). The commonest form is that illustrated in figure 1. The stalk is very short and broad, and the fructification is pulvinate rather than stilboid. The heads vary from 299–1035 μ in height and from 390–1300 μ in diameter, while the stalks vary from 130–650 μ in length and from 234–780 μ in diameter. A whitish sheath, which is more conspicuous in dry specimens, surrounds the stalk and envelops the basal part of the conidial head. When dry the surface of the head, especially in older fructifications, is often flat or slightly cupulate, and the sheath may then appear as a fringe around the margin of the discoid head. When moistened, the head swells, becomes convex, and protrudes from the sheath. According to Petch (22), the sessile or pulvinate form of fructification is characteristic of the fungus in temperate regions. In the tropics they are larger, better developed, and almost always stilboid. From one to sixteen conidial heads may develop on a single scale; usually from two to eight are produced. They project from the margin of the scale, forming a ring partially or completely surrounding it. The bases of the stalks are sometimes united by a stromal band that barely protrudes from beneath the scale. The conidial head may also push through the surface of the scale at any point.

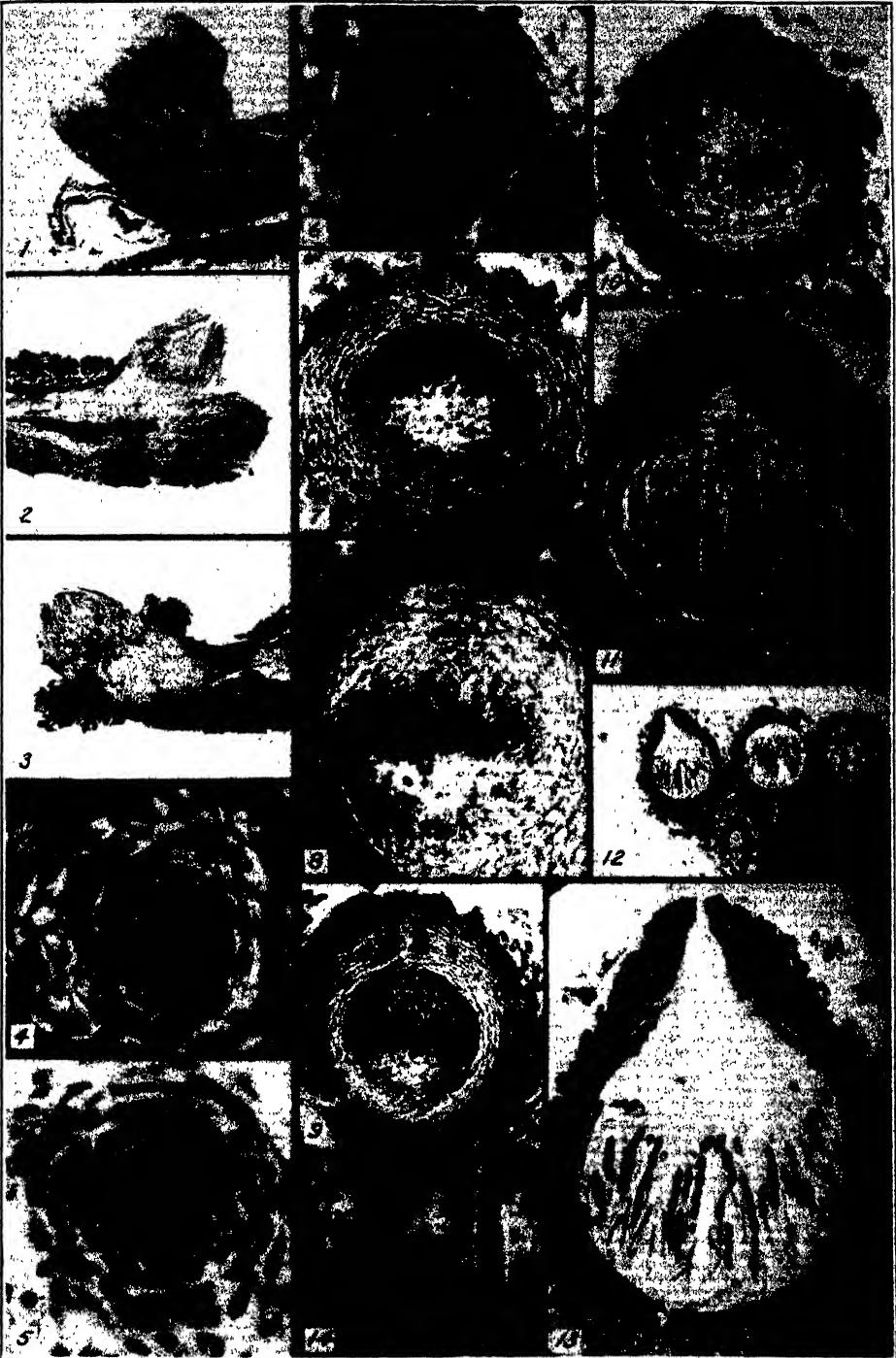
Sections of infected scales show that when the conidial heads appear the fungus has completely destroyed the body of the scale and filled the space between the resistant shield of the scale and the bark with a plectenchymatous stroma (figs. 1, 3). The fungus does not penetrate the bark but attacks only the scale. Its stroma is composed of hyphae of varying diameters which are irregularly and intricately interwoven. The hyphal cells are cylindrical, their cytoplasm is vacuolate and granular, and each contains a single conspicuous nucleus. The conidial fructifications are initiated as protuberances of this stroma. Toward the apex of the protuberance the hyphae become arranged parallel to its axis and separate above to form a fascicle of slender branching conidiophores which are 2.5–5.0 μ in diameter (fig. 2). In the hyphae of the stalk and in the conidiophores the cytoplasm is denser and the nuclei are more deeply staining than in the remainder of the stroma. In the basal part of the head the conidiophores are often joined to one another by ladder-like connections. Conidia are abstricted singly from the tips of conidiophores. In the formation of a conidium the tip of the terminal cell of a conidiophore elongates and increases in diameter. Its

nucleus divides, one daughter nucleus remaining in the base, the other migrating into the elongating tip. A constriction appears at the base of the enlarged terminal portion, and finally a cross wall is laid down in the constriction, cutting off the uninucleate, fusiform young conidium (fig. 38) which has now reached almost its mature dimensions. By division of the primary nucleus the conidium becomes binucleate. Further nuclear divisions and the formation of cross walls were not observed, but the conidium ultimately is divided into 4-11 uninucleate cells. The appearance of conidia divided by four transverse walls into cells much longer than those of mature conidia indicates that cross walls are formed immediately after each nuclear division. Masses of conidia are thus formed in the apex of the head. The mature conidia are 3-10-septate (the majority 5-8-septate) and measure $64-100 \times 5.6-8.4 \mu$. They are hyaline, fusiform, straight or more often curved, and acute at the tips. The proximal end is generally somewhat falcate; the distal end is almost straight (fig. 38).

The peripheral layer of hyphae in the stalk remains sterile and extends upward as a sheath surrounding the fascicle of conidiophores. In the apical portion the sheath is sometimes divided into triangular teeth appressed to the sides of the conidial head. More often, however, the teeth are not distinct, and the sheath terminates in an irregular fringe of hyphae. This observation is in agreement with Petch's (22) description. He found in

Explanation of figures 1-14

All figures photomicrographs. FIG. 1. Conidial fructification of *Sphaerostilbe amanticola* on *Chrysomphalus obscurus*, $\times 40$. FIG. 2 Young conidial heads growing out from beneath the margin of the scale, $\times 40$. FIG. 3. A conidial head with a group of perithecial initials in various stages of development lying in the stroma immediately beneath. The central cavity has been developed in the young perithecium on the lower right, $\times 40$. FIG. 4. An ascogonium embedded in the stroma, $\times 1000$. FIG. 5. An ascogonium surrounded by concentric layers of vegetative hyphae which will form the perithecial wall, $\times 1000$. FIG. 6. Young perithecium. A wall formed by vegetative hyphae encloses the ascogonium, $\times 400$. FIG. 7. Perithecium showing the origin of the vertical hyphae from the inner portion of the perithecial wall. The basal part of the perithecial cavity is occupied by a mass of ascogonial cells which are being emptied of their contents, $\times 400$. FIG. 8. Perithecium in which the vertical hyphae have formed a palisade of parallel hyphae growing downward from the apical portion of the wall. A few 2-4 nucleate cells are scattered among the empty ascogonial cells, $\times 400$. FIG. 9. Perithecium in which the vertical hyphae have almost filled the perithecial cavity. The remains of the emptied ascogonial cells are being crushed at the base of the perithecium. The ostiole is being initiated in the apical region of the wall, $\times 160$. FIG. 10. Perithecium just prior to the formation of asci. The vertical hyphae have increased in diameter to fill the perithecial cavity and their tips have pushed into the base of the perithecium. Formation of the ostiole is in progress, $\times 160$. FIG. 11. Perithecium with young, uninucleate asci growing upward among the vertical hyphae. The ostiole is almost completely formed, $\times 160$. FIG. 12. Group of mature perithecia partially embedded in the stroma, $\times 40$. FIG. 13. Mature perithecium with asci in all stages of development. The vertical hyphae are disintegrating. The ostiole is completely formed, $\times 160$. FIG. 14. Portion of the hymenium showing a uninucleate ascus among the swollen vertical hyphae. The binucleate cell at the base of the ascus is proliferating to form a second ascus by means of a erosier, $\times 1000$.



specimens from tropical regions that the teeth of the sheath were well defined but that they tended to separate into their constituent hyphae in specimens from the temperate zone.

DEVELOPMENT OF THE PERITHECIUM

Perithecia of *Sphaerostilbe aurantiicola* may develop at any time during the year when sufficient moisture is available. Perithecia initiated in the spring become mature during late spring or early summer. There is little further development during the dry summer months, but in the fall activity is usually resumed. As a result of rainy weather during the fall, perithecia were abundant in November and December of 1942. At this time perithecia in all stages of development were present on the infested branches. Indeed, a variety of stages could often be found in sections of a single infected scale. Most of the perithecia were washed away during the winter, but a few mature perithecia were still present the following spring. During the fall of 1943, however, no perithecia developed. This was probably because of long periods of dry weather during that season.

The first indication of perithecial development is the formation of ascogonia within the stroma. Ascogonia are produced in large numbers at the base of the conidiophores, in the periphery of the stalk below the conidiophores, and just below the surface of the stroma at the margin of the scale. They are just beginning to form at the stage of development illustrated in figure 1. A fully developed ascogonium is an intricate, compact coil of enlarged multinucleate cells whose protoplasm is denser and more deeply-staining than that of the surrounding hyphae of the stroma (fig. 4). Each ascogonial cell contains from two to as many as twelve nuclei (fig. 34). Furthermore, the ascogonial nuclei are larger than those of the vegetative cells. The youngest ascogonium observed was a recurved hypha of several slightly enlarged, rather deeply staining, 1-2-nucleate cells, tapering at the base into an ordinary vegetative hypha (fig. 35). Apparently the ascogonium originates from a branch of a vegetative hypha. In its formation the hypha becomes recurved and coils about itself, its cells enlarge, the protoplasm becomes denser, and each cell becomes multinucleate by free nuclear division of the single original nucleus. Neither trichogynes nor spermatia or any sort of antheridial structures with which copulation could take place were observed. There was no evidence of fusions between ascogonia or between cells of a single ascogonium. The nuclei usually do not appear to be arranged in pairs but are irregularly distributed in the ascogonial cells.

The surrounding hyphae of the stroma now produce branches which coil about the ascogonium (fig. 5) and soon enclose it within a spherical envelope composed of several layers of concentrically arranged hyphae (fig. 6). This envelope increases in thickness and develops into the wall of the young

perithecium. At this stage the perithecia begin to protrude from the stroma (fig. 3), and are visible under the hand lens as tiny pimples clustered upon its surface. By continued growth of the hyphae constituting the wall a schizogenous cavity is created in the center of the young perithecium. This cavity becomes filled as it develops, however, for the hyphae making up the inner layers of the wall give off branches which grow inward, their free tips directed toward the center of the perithecium (fig. 7). A difference in rates of growth of these hyphae is soon evident. Those arising from the base and sides of the perithecium grow relatively little, producing a small mass of plectenchymatous tissue in the base of the perithecium below the ascogonium, while those arising from the apical portion of the wall grow rapidly, keeping pace with the expansion of the wall and filling the perithecium with a palisade of simple hyphae arranged parallel to its longitudinal axis. Their attachment to the apical region of the wall is always clearly evident. Their free tips are directed toward the base of the perithecium and press downward against the ascogonium (figs. 8, 36). The terminal cells of these vertical hyphae remain densely filled with protoplasm, while the proximal cells lying toward the apex of the perithecium become vacuolate. The cells are uni- or binucleate (fig. 36).

Meanwhile the ascogonial cells have continued to enlarge. Their protoplasm moves to one side of the cell (fig. 36), and gradually they become emptied, appearing as a hyaline mass of large, thin-walled cells occupying the center of the perithecium. There is little indication that the protoplasm of the ascogonial cells is disintegrating; instead, it appears to be moving out of the cells. On the other hand, there was no clear evidence of the production of branches from the ascogonial cells into which their protoplasm might migrate. Because of the compact arrangement of the ascogonial cells, any branches arising from them would necessarily be extremely tortuous, and it is unlikely that the course of a branch could be followed in sectioned material. Occasionally an ascogonial cell with a protuberance which might represent the basal part of a branch the distal part of which had been lost in sectioning is found. Also, 2-4-nucleate cells provided with a dense cytoplasm appear among the empty ascogonial cells (fig. 36). It seems probable that they are portions of ascogenous hyphae arising from the ascogonium. This has not been demonstrated conclusively, however, and it is possible that the binucleate cells which appear among the ascogonial cells are derived from the deeply staining, often binucleate terminal cells of vertical hyphae which have pushed in to the ascogonial coil. Although the ascogonial cells are long persistent, they are ultimately crushed by the downward growth of the vertical hyphae (figs. 9, 10).

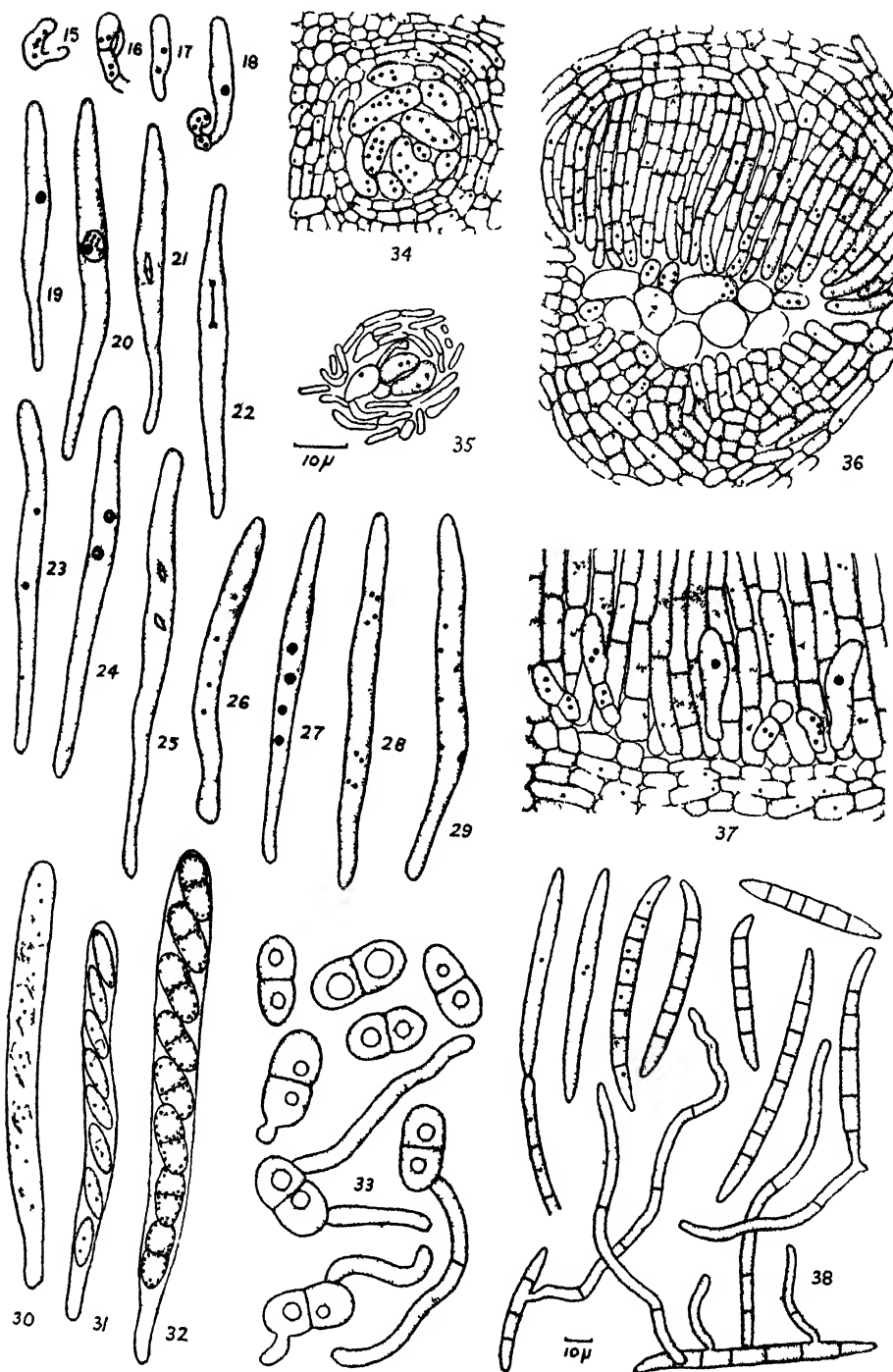
The perithecial wall is now thickened and differentiated into two layers: an inner portion composed of 6-12 layers of hyaline cells which are com-

pressed and flattened by the pressure resulting from the growth of the vertical hyphae within the perithecium, and an outer portion of large, thick-walled, pigmented cells. About the time that the ascogonia disappear the ostiole begins to develop. In the thicker apical region branches of hyphae composing the inner portion of the wall turn upward and begin to grow more rapidly (fig. 9). Their upward growth produces a papilla, and by their pressure against one another the hyphae in the core of the papilla are separated, forming an ostiole lined with free hyphal ends (figs. 10, 11).

While the ostiole is forming, the vertical hyphae within the perithecium continue growing until they extend to the bottom of the perithecium. Their tips press into the plectenchymatous tissue lining the basal portion of the perithecial wall so that they are attached both above and below (fig. 10). They now swell, and the protoplasm of their cells becomes thin and vacuolate. Each cell contains one or several nuclei (fig. 37). In the plectenchyma lining the base of the perithecium among the tips of the vertical hyphae are binucleate cells, appearing singly or in chains of two or three cells (fig. 37). These presumably are the ascogenous cells mentioned above as probably being derived from the ascogonium. Whatever their origin, they now proceed to form asci by means of croziers. As the asci develop the perithecium continues to enlarge. The vertical hyphae separate and gradually disintegrate, leaving a cavity above the asci (figs. 11, 13). Even now their attachment to the apical portion of the wall is still clearly evident. Although they resemble paraphyses, in view of their origin, it is clear that they are not true paraphyses. They constitute a nurse tissue within which the asci develop. Paraphyses are never formed in *Sphaerostilbe auranticola*. As the asci ma-

Explanation of figures 15-38

Camera lucida drawings. Fig. 38 to the scale shown in the same figure, all others to the scale shown in fig. 35. Figs. 15-32. Development of the ascus. FIG. 15. Initiation of crozier. FIG. 16. Crozier. The ultimate cell of the crozier has fused with, and its nucleus has passed into, the basal cell. FIG. 17. Young ascus prior to fusion of the two nuclei. FIG. 18. Young ascus in which the two nuclei have fused. The binucleate basal cell is proliferating to form a second crozier. FIG. 19. Young ascus with enlarged fusion nucleus. FIG. 20. Early prophase of 1st division. FIG. 22. Late anaphase of 1st division. FIG. 23. 2-nucleate ascus. FIG. 24. Prophase of 2nd division. FIG. 25. Early anaphase of 2nd division. FIG. 26. 4 nucleate ascus. FIG. 27. Prophase of 3rd division. FIG. 28. Telophase of 3rd division. FIG. 29. Eight-nucleate ascus. FIG. 30. Ascus in which cleavage furrows are cutting out eight ascospores. Each ascospore nucleus has already divided to form two daughter nuclei. FIG. 31. Ascus with young unicellular spores. FIG. 32. Ascus with eight almost mature two-celled ascospores. FIG. 33. Mature ascospores after discharge from the ascus and stages in their germination. FIG. 34. Ascogonium embedded in the stroma. FIG. 35. Young ascogonium. FIG. 36. Section of young perithecium showing the palisade of vertical hyphae growing downward into the perithecial cavity. 2 and 4-nucleate cells appear among the empty ascogonial cells. FIG. 37. Section of the base of a perithecium in which asci are forming among the swollen vertical hyphae. FIG. 38. Origin of conidium from tip of conidiophore, mature conidia, and germination of conidia.



ture the inner hyaline portion of the wall is crushed and flattened against the darkened outer portion, leaving a relatively thinner wall enclosing an enlarged central cavity. The mature asci occupy the lower two-thirds of this cavity (fig. 13). They are $112\text{--}154\ \mu$ long and $14\text{--}16.8\ \mu$ in diameter. Each contains eight hyaline, elliptical to oblong, two-celled ascospores measuring $12.5\text{--}18.7 \times 7.2\text{--}10\ \mu$. The ascospores are uniseriately arranged within the asci.

Mature perithecia are roughly spherical to ovate with a slight papilla penetrated by a periphysate ostiole at the apex and are $273\text{--}377\ \mu$ in diameter. They are pale-rose-colored when dry, but they become bright red when moistened. The perithecia are usually clustered upon the stroma in which their basal portions are embedded (fig. 12), and they often are grouped around the old conidial fructifications. When only a few perithecia are formed, they may appear scattered over the surface of the scanty stroma.

Each perithecium arises from a single ascogonium. The ascogonia are numerous, however, and not all of them develop into perithecia. Sections have been examined which showed an ascogonium being enclosed by the wall of another perithecial initial in a more advanced stage of development. The included ascogonium was disintegrating. Another abnormality observed was produced from two perithecia developing in proximity. Their adjacent walls had fused and become compressed and partially disintegrated. Although the two perithecia possessed one common perithecial cavity, each formed its separate ostiole.

CYTOLOGY OF THE ASCUS

The asci of *Sphaerostilbe aurantiicola* arise from binucleate cells in the plectenchyma lining the base of the perithecium. Although slightly bowed 4-nucleate cells whose appearance suggested that of croziers were observed arising from the ascogenous cells (fig. 37), no structures which could be identified positively as croziers were found in the stained sections. Recourse was, therefore, had to smears and mounts of perithecia teased apart. In such mounts it was occasionally possible to demonstrate the presence of croziers. In the production of an ascus a binucleate ascogenous cell elongates and becomes bowed while the two nuclei divide to form four (fig. 15). This four-nucleate cell is now divided by two cross walls into a basal uninucleate cell, an apical uninucleate cell, and a median binucleate cell. The apical cell recurves and fuses with the basal cell, and its nucleus passes into the basal cell (fig. 16). The median cell elongates to form the young binucleate ascus (fig. 17), while the now binucleate basal cell may proliferate to form a second ascus (figs. 14, 18).

The two nuclei in the young ascus fuse to form a single larger fusion nucleus. Initially the fusion nucleus is homogeneous (figs. 18, 19), but as it

enlarges its structural detail becomes evident (fig. 20). The nuclear membrane, a single conspicuous nucleolus, and several chromatin threads may be distinguished. No centrosomes were observed in the interphase nuclei nor during the prophase. The next stage observed was a metaphase of the first division (fig. 21). The spindle lay in a clear area in the cytoplasm, oriented parallel to the longitudinal axis of the ascus and was no longer than the diameter of the original nucleus. The nucleolus had disappeared. Tiny black masses observed at either end of the spindle probably represent centrosomes. At the equator of the spindle were two chromatic masses each of which possibly comprised two chromosomes since, as will be noted later, two such masses were observed migrating to each pole during the anaphase of the second division. It is probable that the chromosome number is two although the smallness of the division figures makes certainty of this impossible. At any rate, the chromatin masses move to the poles while the spindle elongates and appears as a dark strand between the two masses (fig. 22). From these two chromatin masses two daughter nuclei are reorganized. The interphase nuclei are small and homogeneous (fig. 23). As they prepare for the second division they enlarge, although even so their diameters are less than half that of the primary fusion nucleus. In the prophase the nuclear membrane, chromatin threads and nucleolus are once more discernible (fig. 24). The next stage observed was an anaphase of the second division showing two spindles slightly oblique in orientation to the ascus. In each figure there were two chromosomes passing to either pole (fig. 25). The four nuclei reorganized from the second division were also small and homogeneous (fig. 26). As they entered the prophase of the third division they enlarged slightly and their internal structure became apparent (fig. 27). The only stage of the third division observed was a telophase (fig. 28) in which the position of the eight chromatin masses indicated that the orientation of the spindles had been oblique.

After the third division of the fusion nucleus, eight homogeneous daughter nuclei are reorganized (fig. 29). Cleavage furrows then cut out an elliptical ascospore around each nucleus. There was no evidence that astral rays function in the delimitation of the ascospores. Each nucleus divides immediately, often before the outlines of the ascospore are clearly visible, to form the two nuclei of the ultimately two-celled ascospore (figs. 30, 31). An oil globule now forms at each end of the ascospore. The two nuclei migrate toward opposite ends of the ascospore, and a cross wall is laid down, dividing the spore into two cells. The oil vacuoles enlarge, and the cytoplasm becomes granular and filled with chromatic masses so that the nucleus is obscured (fig. 32). The interval between the uninucleate ascus and the formation of spores must be short, as it was difficult to find intermediate stages.

SPORE GERMINATION AND GROWTH IN CULTURE

Cultures of *Sphaerostilbe aurantiicola* were obtained from conidia by streaking a conidial suspension upon agar plates and from ascospores by suspending mature perithecia from the top of a Petri dish so that the spores were discharged upon the agar below. Both types of spores germinated overnight although the conidia germinated more rapidly than did the ascospores. Any of the three to twelve cells of the conidium may produce a single germ tube (fig. 38). Usually, several germ tubes originate from each conidium. Often certain cells in the conidium, either terminal or intercalary, appeared narrower and less swollen than the remainder of the cells. This apparently is of no significance, since the narrow cells produced germ tubes as readily as the swollen cells. Conidia produced in masses in cultures in which the nutritive medium is already covered by mycelium may germinate to form secondary conidia similar to the primary conidia. Secondary conidia are probably produced similarly in nature by conidia that fall upon substrates unfavorable for their growth. In germination either cell of the ascospore may produce a single germ tube. One or two germ tubes arise from each ascospore (fig. 33).

The fungus was cultured on potato dextrose agar, malt agar, and on acidulated bread, as suggested by Rolfs (23). It grew equally well on all three media. The average rate of growth at room temperature as determined from measurements of fifty-three colonies in three series of experiments conducted at different times was 0.782 mm. per day. The differences in rates of growth of colonies kept in total darkness and those given various daily exposures to light from five minutes to a full day were extremely slight and variable. It is concluded that light has no effect upon rate of growth in culture.

Although light has no influence upon rate of growth, it does have a pronounced effect upon character of the mycelium produced. In cultures maintained in total darkness the mycelium is thick and fluffy, forming sharply delimited pulvinate colonies, while in those exposed to light it grows closely appressed. This difference in type of growth results in distinct zonation in colonies kept in the laboratory where they were exposed to daily alternations of light and darkness. Colonies kept in total darkness and removed for measurement every two days also exhibited zonation, although there were only half the number of concentric rings in these colonies as in those exposed to natural illumination. The brief exposure to light of not more than ten minutes every forty-eight hours necessary for making measurements was sufficient to induce zonation.

Light modifies also the production of conidia in culture. Colonies kept in total darkness for one month produced no conidia, while those exposed to light developed conidia within eight days. Experiments in which series of

cultures of five each were kept in total darkness or exposed to the light from a north window of the laboratory for periods of five, fifteen, thirty, and sixty minutes daily showed that exposure to light for as short a period as five minutes daily resulted in the formation of conidia. The conidia are formed in orange masses lying in concentric rings corresponding to the zonation of the mycelium. They are identical with those formed in nature, and no other spore form is produced. Penicillium-like spores described by Rolfs (23) have not appeared in my cultures.

A few scattered perithecia formed in old cultures on potato dextrose agar, but these never produced ascospores.

PERITHECIAL DEVELOPMENT IN THE HYPOCREALES

Archicarps. Initiation of perithecia without the intervention of archicarps has been reported for only two species of Hypocreales, *Nectria Ipomoeae* Halst. [*Hypomyces Ipomoeae* (Halst.) Wr.] and *Nectria galligena* Bres. Cook (5) was unable to find them at any stage in the development of perithecia of *Nectria Ipomoeae*. According to Cayley (4), the perithecium of *Nectria galligena* originates as a globular mass of vegetative hyphae which becomes differentiated into a perithecial wall and a central tissue of thin-walled cells. Later an ascogonium develops within the young perithecium. It seems probable that in these two species the early stages of ascogonial formation have been overlooked, for in all other species the perithecium is always initiated by an archicarp. Furthermore, there is considerable uniformity in its structure in the various species. As in *Sphaerostilbe auranticola*, it is usually in the form of an ascogonium composed of a coil of enlarged binucleate or multinucleate cells differentiated from the vegetative cells by their larger size, their more deeply staining protoplasm, and the number and size of their nuclei. Such ascogonia have been described in *Nectria Ribis* (Tode) Rabenh. (Vincens 27), *Hypocrea gelatinosa* (Tode) Fr. (Vincens 27), *Thyronectria denigrata* (Wint.) Seaver (Lieneman 16), *Pezizella lateritia* (Fr.) Maire (Moreau 20), *Cordyceps agariciformis* (Bolt.) Seaver (Jenkins 14), *Cordyceps militaris* (L.) Link (Varitchak 25, 26), *Claviceps microcephala* (Wallr.) Tul. (Vincens 27), *Claviceps purpurea* Tul. (Killian 15), and *Epichloe Bambusae* Pat. (Gäumann 12). The ascogonium of *Polystigma rubrum* DC. (Nienburg 21) is similar except that it terminates in an elongated trichogyne.

Origin and Sexuality of Archicarps. In all species studied, whether their mature perithecia are immersed within a well-developed stroma as in *Hypocrea*, *Claviceps*, and *Epichloe* or merely clustered upon the surface of a stroma as in *Sphaerostilbe* and *Thyronectria*, the ascogonia are formed within a stroma. Formation of the ascogonium generally seems to be similar

to the process described in *Sphaerostilbe aurantiicola*. A branch of a vegetative hypha enlarges, becomes more deeply staining, and coils. The cells become multinucleate by free nuclear division. Generally there are no fusions between ascogonia, between cells of a single ascogonium, or between ascogonia and other reproductive structures. *Polystigma rubrum* (Nienburg 21) and *Epichloe Bambusae* (Gaümann 12) are to be noted as exceptions in which fusions between cells of the ascogonium have been reported. Fusion of the ascogonium with an antheridium has been described in *Claviceps purpurea* (Killian 15), *Claviceps microcephala*, and *Hypocrea gelatinosa* (Vincens 27). Although *Polystigma rubrum* produces spermatia coincidentally with the ascogonia, the spermatia at present are considered to be non-functional. Early observers (Fisch 9, Frank 11) believed the spermatia and trichogynes to be functional, but later workers have disagreed. Blackman and Welsford (2) were unable even to trace the trichogyne to the surface of the stroma; and while Nienburg (21) found that the tip of the trichogyne projected from the surface of the stroma, he also considered it to be non-functional. Lack of accord in the observations of different mycologists upon the same or related species shows that satisfactory cytological evidence for the functioning of supposed sexual organs is often difficult to obtain. Consequently, some doubt must exist as to the extent of the occurrence of sexual fusions in the Hypocreales.

The problem of sexuality may be more successfully attacked in heterothallic species in which the results of genetical experiments may be correlated with cytological evidence. Heterothallism has been reported in several species of Hypocreales; but, unfortunately, the morphological basis of sexuality in these species has not yet been determined. Dimock (7) described the occurrence of two mutually compatible, hermaphroditic but self-sterile strains in *Hypomyces Ipomoeae* (Halst.) Wr. When cultured from monosporous isolations, each strain produced perithecial initials, but these did not develop into mature perithecia. When opposite strains were mated, however perithecia developed. Dimock (7) found also that he could induce formation of perithecia by placing a suspension of microconidia from one strain upon the mycelium of the opposite strain. “. . . , perithecia developed only on those portions of the colony which had actually been wetted by the microconidial suspension. When single drops of spore suspension were added, perithecia developed only within the limits of the drop.” *Hypomyces rosellus* (Alb. & Schw.) Tul. (Zycha 29) and *Hypomyces Solani* f. *Cucurbitae* (Hansen & Snyder 13) also have been proved to be heterothallic. Careful morphological studies of these heterothallic species will probably demonstrate the presence of functional trichogynes which fuse with either micro- or macroconidia.

Perithecial Wall. Whatever the sexual nature of the ascogonia, it is certain that they are the centers around which the perithecia develop. Only a single ascogonium may be involved in the formation of a perithecium, as in *Sphaerostilbe aurantiicola*, or as many as three distinct ascogonia may function in the formation of a single perithecium, as in *Cordyceps agariciformia* (Jenkins 14). The ascogonia early become invested by layers of sterile hyphae which may originate from the ascogonial stalks or from branches of the surrounding vegetative hyphae. This envelope of sterile hyphae surrounding the ascogonium increases in thickness, and by growth of its constituent hyphae it expands to form a flask-shaped wall enclosing the perithecial cavity. At the apex a papilla penetrated by a schizogenously formed ostiole lined with periphyses develops. When the perithecia remain immersed within the stroma at maturity, the perithecial walls are sometimes not well developed. Vincens (27) states that the perithecial wall of *Hypocrea gelatinosa* is thin and poorly delimited at the periphery. This is true also of species belonging to the Claviceptaceae. In the most extreme example described, *Epichloe typhina* (Vincens 27), a perithecial wall is not developed at all, the expansion of the ascogenous hyphae and asci merely creating an unwalled locule in the stroma. According to Brandriff (3), perithecial walls are lacking also in *Acrospermum compressum* Tode.

Ascogenous Hyphae. As the perithecial wall forms, the ascogonia continue their development within the perithecium. Generally, ascogenous hyphae arise as branches of the ascogonial cells. It is, however, often exceedingly difficult to trace all of the stages in this process. My observations upon *Sphaerostilbe aurantiicola* incline me to believe that the ascogenous hyphae in this species are produced from the ascogonia, although it has been impossible to demonstrate this satisfactorily. The evidence obtained might be interpreted as indicating that the ascogonia disintegrate after serving as stimulatory organs for the initiation of the perithecia and that the ascogenous hyphae arise subsequently from hyphae derived from the wall in the base of the perithecium or from the often binucleate terminal cells of the vertical hyphae. Both of these interpretations have been applied previously to various species. In *Hypocrea gelatinosa* (Vincens 27), *Peckiiella lateritia* (Moreau 20), *Cordyceps agariciformia* (Jenkins 14), *Cordyceps militaris* (Varitchak 25, 26), *Claviceps microcephala* (Vincens 27), *Claviceps purpurea* (Killian 15), *Epichloe typhina* (Vincens 27), and *Epichloe Bambusae* (Gäumann 12) reports indicate that the ascogenous hyphae arise from the ascogonia or from certain cells of the ascogonia. This appears to be true also of *Nectria galligena* although Cayley (4) in an ambiguous statement indicates that the ascogenous hyphae in this species arise de novo from hyphae in the base of the perithecium. On the other hand, Vincens (27) states that

in *Nectria Ribis* the ascogonia disintegrate completely and that ascogenous hyphae arise from ordinary hyphae in the base of the perithecium. A similar process is reported by Blackman and Welsford (2) for *Polystigma rubrum*. Nienburg (21), however, in a study of the same species found that the ascogonium does not disintegrate completely but that one cell of the ascogonium continues its development and gives rise to ascogenous hyphae. Although it is possible that in some species of Hypocreales the ascogonia may no longer be functional in the production of ascogenous hyphae, nevertheless, the difficulties in tracing their development may be responsible for the conclusion that they are functionless.

Paraphyses. According to Miller's (18) definition of a perithecium, an essential characteristic is the presence of paraphyses in the centrum. This is true of *Nectria galligena* (Cayley 4) and *Hyomyces aurantiis* (Vincens 27). Paraphyses are present also in *Thyronectria denigrata* (Lieneman 16), but they are unusual in that, while they arise from the base and sides of the perithecium, they are branching anastomosing structures embedded in a gelatinous matrix. No mention of paraphyses is found in the papers of Blackman and Welsford (2) on *Polystigma rubrum* and of Moreau (20) on *Pickiella lateritia*. Paraphyses are not, however, uniformly present in the Hypocreales. Paraphyses do not occur in the perithecia of the Claviceptaceae including the species mentioned above under the genera *Claviceps*, *Claviceps* and *Epichloe*. In these species the ascogenous hyphae occupy the basal portion of the perithecial cavity, and the asci grow up into the cavity as it develops. Paraphyses are lacking also in *Hypomyces rosellus* (Zycha 29). According to Cook (5), the perithecia of *Nectria Ipomoeae* are aparaphysate. The young perithecium is filled with a mass of thin-walled pseudoparenchyma. Asci originate in the base of the perithecium and push up into this pseudoparenchyma which is crushed and disintegrated as the asci mature. In *Sphaerostilbe aurantiicola* the perithecial cavity is filled by a mass of vertical hyphae originating from the ostiolar region of the perithecial wall. The resemblance of these hyphae to the vertical hyphae in the ascocarp of *Sporormia leporina* Niessl. as described by Arnold (1) is worthy of mention. The latter have been considered pseudoparaphyses by Miller (19). Since pseudo paraphyses have been reported only in species with stromatic ascocarps which presumably lack perithecial walls and since the nature of pseudoparaphyses is not yet clearly understood, it seems advisable at present to designate the palisade-like mass of vertical hyphae in the perithecium of *Sphaerostilbe aurantiicola* simply an ascocal nurse tissue. The type of perithecium illustrated by *Sphaerostilbe aurantiicola* is not unique among the Hypocreales. My own unpublished observations indicate that the perithecium of *Creonectria purpurea* (L.) Seaver has a similar structure. In addition, Vincens' figure of an

early stage of perithecial development in *Nectria Ribis* (27, fig. 40) shows a striking resemblance to my figure 36. of *Sphaerostilbe aurantiicola*. Here also may be seen the palisade of vertical hyphae growing downward from the ostiolar region of the wall to fill the perithecial cavity. Vincens states that later true paraphyses originate in the base of the perithecium, but his fig. 41 of a perithecium in which asci are developing shows the perithecium still filled with vertical hyphae attached to the apical part of the wall. He records a similar condition of *Hypocrea gelatinosa* (27).

Crozier Formation. Accounts of the origin of the ascus are at variance. Vincens (27) stated that no croziers were observed in *Hypomyces aurantius* or in *Nectria Ribis*. In *Claviceps microcephala* and *Epichloe typhina* (27) he described the asci as originating from direct outgrowths of binucleate cells, but Dangeard (6) found that in the latter species asci are formed from croziers. Jenkins (14) reported that the asci of *Cordyceps agariciformia* may be formed either from croziers or directly. Croziers have been described in *Peckiella lateritia* (Moreau 20), *Thyronectria denigrata* (Lieneman 16), *Hypomyces Thiryanus* (Maire 17), *Cordyceps militaris* (Varitchak 25, 26), *Claviceps purpurea* (Killian 15), and *Epichloe Bambusae* (Gäumann 12). Formation of asci from croziers was observed in *Sphaerostilbe aurantiicola* if the hymenium was teased apart although it was impossible to demonstrate them satisfactorily in sectioned material. This indicates that it might be possible to demonstrate croziers in other species in which they have not been observed if proper methods were employed. It is probable that formation of asci from croziers is characteristic of the order.

Cytology of the Ascus. In the few species of Hypocreales upon which studies of the cytology of the ascus have been made there is the usual fusion of two nuclei in the young ascus to form a single fusion nucleus which enlarges and undergoes three successive divisions. There is no evidence of nuclear fusions other than those which occur in the young ascus at any stage in the life history of any species studied. Consequently, there is probably only a single meiosis prior to spore formation in the ascus. The division figures are small, and it is difficult to distinguish chromosomes with certainty. Chromosome counts have, however, been made previously for three species. According to Maire (17) the chromosome number of *Hypomyces Thiryanus* is four. The counts of Jenkins (14) upon *Cordyceps agariciformia* and of Varitchak (26) upon *Cordyceps militaris* agree with my own upon *Sphaerostilbe aurantiicola*. In these three species the chromosome number appears to be two. In *Sphaerostilbe aurantiicola* as in *Cordyceps agariciformia* (Jenkins 14) there is no evidence that astral rays function in spore delimitation. Cleavage furrows resulting from vacuolization cut out the ascospores. The ascospores of *Hypomyces Thiryanus* (Maire 17) and of *Cordyceps*

militaris (Varitchak 26), however, have been reported to be delimited by astral rays. Observation of such structures may be conditioned by the technical methods employed.

DISCUSSION

From a consideration of the preceding review of perithecial development in the Hypocreales it seems that at least the following five types of ascocarp may be recognized in this order:

1. Asci formed in perithecia consisting of a perithecial wall perforated by a periphysate ostiole and lined in the basal region with a hymenium of paraphyses and asci. *Nectria galligena*, *Hypomyces aurantius*, *Thyronectria denigrata*.

2. Perithecial wall and ostiole present, paraphyses lacking, perithecial cavity filled with a palisade of simple hyphae growing downward from the apical region of the perithecial wall and forming a nurse tissue for the asci which grow up among them. *Sphaerostilbe auranticola*, *Nectria Ribis* (?), *Hypocrea gelatinosa* (?), *Creonectria purpurea*.

3. Perithecial wall and ostiole present, paraphyses lacking, asci formed within a pseudoparenchymatous tissue which fills the young perithecium and disintegrates as the developing asci push up into it. *Nectria Ipomoeae*.

4. Perithecial wall present but often poorly developed, ostiole present, paraphyses lacking, asci filling the perithecial cavity as it develops. *Cordyceps militaris*, *Cordyceps agariciformia*, *Claviceps purpurea*, *Claviceps microcephala*, *Epichloe Bambusae*.

5. Asci formed in locules within a stroma, arising in groups within the stroma and by their growth creating the locules, perithecial wall, ostiole, and paraphyses lacking. *Epichloe typhina*.

Miller (19) has given the following definition of a perithecium: "True perithecia with walls that arise from the basal cells of the archicarp, the upper wall cells proliferating upward to form a definite ostiole, asci forming a wall layer, interspersed with true paraphyses in the ostiolar canal." In another paper (18) he stated, "When there is a true wall there is no pseudoparenchyma in the centrum, there are true paraphyses and periphyses, concave hymenial layer, and the ostiolum is schizogenous in type." While this definition is satisfactory for the majority of perithecia, there are many variations in perithecial structure which it does not recognize. It is evident that the type of centrum described by Miller is not characteristic of all perithecia. Upon the basis of structure of the centrum, perithecia of species in the Hypocreales may be separated into four groups illustrated by the above mentioned types 1, 2, 3, and 4.

The only character common to all perithecia is the perithecial wall penetrated by a schizogenously-formed, periphysate ostiole. In some species the wall may be derived entirely from the stalk cells of the archicarp; in others

it is certainly derived, at least in part, from adjacent vegetative hyphae. In either case formation of an archicarp is generally the stimulus for the initiation of the perithecial wall. Cayley's (4) observations upon *Nectria galligena* suggest, however, the possibility that in some species perithecial wall may be initiated prior to the formation of archicarps. The perithecial walls of some species are not well developed. In *Epichloe typhina*, the species upon which the above type 5 is based, they are lacking entirely. Yet in characteristics other than the presence of a perithecial wall (nature of the stroma, development of asci, and type of ascospores) it is clearly related to the Claviceptaceae. In the Claviceptaceae, and possibly in other groups, there has apparently been a reduction in the perithecial wall resulting in the production of stromatic ascocarps.

SUMMARY

Sphaerostilbe aurantiicola (B. & Br.) Petch is a Hypocreaceous fungus which occurs throughout the world as a parasite upon various species of scale insects. It is of economic importance in the control of the San Jose scale in Florida. The present observations upon its morphology are based upon material from the obscure scale [*Chrysomphalus obscurus* (Comst.)] of water oak (*Quercus nigra* L.) in Georgia.

The fungus completely destroys the body of the infected scale and forms a plectenchymatous stroma between the shield of the scale and the bark of its host. It does not penetrate the bark.

Pulvinate or stilboid outgrowths of the stroma from the margin or through the surface of the scale produce clusters of conidiophores which abstrict fusiform conidia from their tips.

Perithecia are initiated by coiled ascogonia composed of enlarged, deeply staining, multinucleate cells which are formed within the stromatic stalk below the conidial head or in the margin of the stroma. Branches of the surrounding vegetative hyphae invest the ascogonium to form the perithecial wall. From the ascogonial cells arise ascogenous hyphae which later produce asci by means of croziers. The ascogonia disintegrate. No paraphyses are formed. Instead, the perithecial cavity is filled by a palisade of vertical hyphae that grow downward from the apical part of the wall of the perithecium and form a nurse tissue for the asci. A paraphysate, schizogenously formed ostiole develops at the apex of the perithecium. At maturity the perithecia are clustered upon the surface of the stroma in which their basal portions are embedded. Although this type of perithecial development has not previously been described, it evidently occurs in other species of Hypocreales.

Sphaerostilbe aurantiicola has been obtained in culture from both conidia and ascospores. The character of the mycelium and the formation of

conidia in culture are dependent upon exposure to light. Light has no effect upon rate of mycelial growth in culture.

From a review of the literature on perithecial development in the Hypocreales and a comparison of other species with *Sphaerostilbe aurantiicola* it appears that five different types of ascocarpic structure may be recognized in this order.

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THE CYTOLOGICAL EFFECTS OF BENZENE VAPOR¹

C. A. BERGER, E. R. WITKUS AND B. J. SULLIVAN

During the past year the cytological effects of several alkaloids, growth-promoting substances, and other chemical agents have been studied in this laboratory. Several of these substances contained in their respective molecules one, two, or three benzene rings and it occurred to one of us² that the effect of benzene itself should be investigated.

The common onion, *Allium cepa*, with the diploid chromosome number of sixteen, was used. Bulbs with young actively growing roots were placed on small beakers nearly filled with benzene. After an immersion of one hour aceto-orcein smear preparations of the root tips revealed cytological effects strikingly similar to those of colchicine, acenaphthene, and other polyploidy-inducing agents. Spindle formation was inhibited, diplo-chromosomes were formed, and tetraploid cells resulted. Liquid benzene was a powerful agent and roots treated by immersion for periods longer than one hour did not recover. It was noted, however, that young roots, too short to come into contact with the liquid benzene but growing in an atmosphere saturated with benzene vapor, developed the same type of cytological effects. Accordingly a new series of experiments was made in which roots were subjected to benzene vapor for periods of from one to six hours. It was found that the roots dried after three hours exposure to benzene vapor but this difficulty was overcome by placing the benzene vessel and the bulb in a larger closed jar containing some water. Three hours treatment with benzene vapor was found to give the best results; marked effects were obtained and the roots recovered and underwent further mitoses.

OBSERVATIONS

The most noteworthy effect of benzene treatment is a precocious separation of chromatids and a clear demonstration of half-chromatids. This effect was more evident after treatment by immersion in liquid benzene than after subjection to benzene vapor. Many cytologists believe that somatic metaphase chromosomes are quadripartite, consisting of two chromatids and four half-chromatids (see review paper of Nebel 1939), but visible evidence of this condition is difficult to obtain. In this material, after one hour of treatment with liquid benzene and no recovery period, the presence of half-chromatids is unmistakable. At late prophase, prometaphase, and early metaphase (figs. 1, 2, 3) chromatids are widely separated on both sides of the

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² Dr. E. R. Witkus.



FIGS 1-9 Mitosis in *Allium cepa* after treatment with benzene. All photomicrographs have a magnification of $\times 1000$ except figure 2 which is $\times 1200$. FIG 1 Late prophase. FIG 2 Prometaphase. FIG 3 Metaphase. FIG 4 Late metaphase, diplo chromosomes. FIG 5 $4n$ chromosomes after delayed division of SA regions. FIG 6 Early reversion stage. FIGS 7 8 9 Reversion stages.

undivided SA-region (spindle attachment region) and are relationally coiled. In favorable preparations each chromatid is clearly seen to consist of two threads (figs. 1, 2, 3). Sister half-chromatids appear to be in paranemic relationship but the smallness of the structures does not permit absolute certainty on this point.

Other effects of benzene and benzene vapor are as follows. As with colchicine, acenaphthene, and other chemical agents the division of the SA-region is delayed by one hour of immersion in liquid benzene or from one to three hours of vapor treatment, and the metaphase chromosomes continue to contract, forming typical diplo-chromosomes (fig. 4). This supercontraction may continue, resulting in very short, thick diplo-chromosomes with widely divergent arms as reported for colchicine-treated material (Levan 1938; Berger & Witkus 1943 and others). The SA-region eventually divides and the tetraploid number of chromosomes are scattered throughout the cell (fig. 5). The achromatic spindle is either prevented from forming or destroyed and there is no anaphase movement of the chromosomes, no daughter telophase nuclei, and no cell plate formation. The chromosomes, either scattered or loosely clumped, begin the reversion process which will result in a tetraploid resting nucleus. The chromosomes begin to despiralize and to assume the structural details of anaphase and telophase chromosomes (figs. 6, 7). Tetraploid telophase nuclei are frequently irregular in shape (figs. 8, 9). The above-mentioned effects are all found in material fixed immediately after treatment and allowed no period of recovery.

Cells that were not in mitosis during treatment do not become polyploid and begin to divide as soon as the roots are placed in water. Many diploid mitoses are found in the first hour of recovery. Cells that were in division during treatment and had become tetraploid do not undergo mitosis during the first three days of recovery but after that period tetraploid mitosis is found. Thus while the root as a whole recovers quickly, the cells which became tetraploid during the treatment require several days to adjust themselves to the newly acquired tetraploid nuclear condition before they are again ready for mitotic division.

SUMMARY

1. Benzene and benzene vapor produce cytological effects similar to those produced by colchicine.
2. Spindle formation is inhibited and division of the SA-region is delayed. Diplo-chromosomes are formed and tetraploid cells result.
3. In root tip divisions in *Allium*, chromatids are widely separated and half-chromatids become clearly visible at prometaphase.

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MORPHOLOGY OF THE RICE SPIKELET

VIRGINIA MICHAUD¹

Some greenhouse plants of *Oryza sativa* have recently produced anomalous structures which may prove helpful in clarifying the morphology of the rice spikelet. The culture, which originated from the caryopses of plants collected by Charles DeVol in China in 1940, has reseeded from time to time and maintained itself for three years.

The single flower of a normal rice spikelet (fig. 1) is enclosed in two indurated bracts; one of these is in the position of a lemma and has the characteristics of a lemma, but the other, which is in the position of a palea, is unlike a palea in that it is single-keeled. Below these are two very small bracts which remain attached at the base of the lemma when the mature fruit disarticulates. Beneath the articulation is a structure which forms a sort of cup around the base of the spikelet.

The rice spikelet has long been a subject of special interest to grass morphologists. The most commonly accepted interpretation regards the two small bracts just above the articulation as glumes, the lower of the two bracts surrounding the flower as the lemma, and the upper as the palea. In most taxonomic works no particular significance is attached to the structure below the articulation. Among the interpretations differing from this there are two which are important.

Mrs. Arber (1934, p. 184) regards the cup below the articulation as the equivalent of a pair of extremely reduced glumes, the next two bracts as sterile lemmas, and the last two as a lemma and a palea. Eichler's diagram (1875, p. 125) of the rice spikelet indicates six bracts, four of which are called glumes. Schuster (1910) interprets this to mean that there are two bracts (stunted glumes) below the structures ordinarily regarded as glumes, these presumably represented by the cup below the articulation.

The second interpretation involves the identity of the upper two bracts. In a hypothesis recently and independently put forth by two workers, N. F. Peterson (1935), of the Univ. of Nebraska, and L. R. Parodi (1939), of Argentina, it is proposed that the spikelet is not one-flowered but represents the union of two florets in which the paleas of both and the pistil of one have disappeared. The two bracts enclosing the flower are then considered as the two fertile lemmas. Parodi (1941) found support for his idea in abnormal spikelets in which he observed two pistils and two linear, binerved paleas

¹ The writer wishes to express her appreciation to Dr. Paul Weatherwax for his helpful suggestions in the preparation of the manuscript.

within the covering of the two rigid bracts. In his description there is no reference to structures below the lower lemma. A similar spikelet is pictured in cross section by Schuster (1910, fig. 14), but he does not explain the figure.

The four abnormal spikelets which I have found give evidence in support of Mrs. Arber's interpretation and raise a question concerning the explanation given by Peterson and by Parodi. All of the spikelets had either more than one flower or more than two indurated bracts. The lower floret of one spikelet contained a flower with a pistil, two lodicules and two stamens. The pistil had four styles. Both the lemma and the palea were indurate and carinate. One stamen was in the normal dorsal position, and the other was in the median position directly opposite. The upper floret was normal. An empty bract was present below the lower lemma.

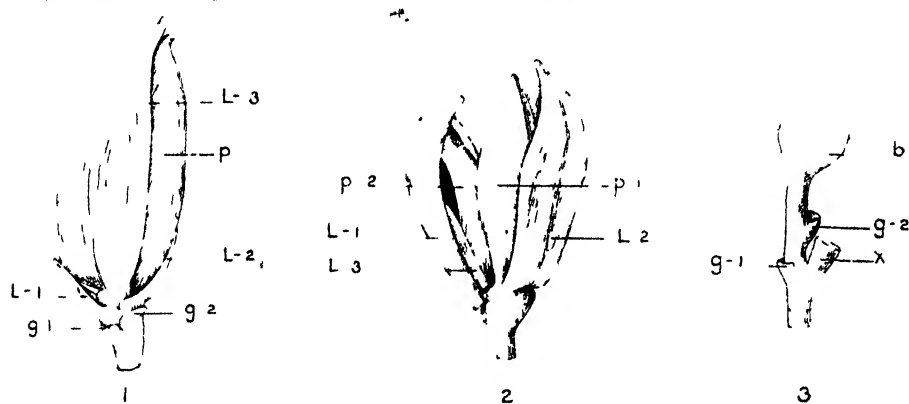


FIG. 1 Normal spikelet of rice. FIG. 2 Portion of abnormal spikelet showing three well developed lemmas and two paleas. FIG. 3. Portion of abnormal spikelet below lemmas. b, base of first lemma; L-1, L-2, L-3, first, second and third lemmas respectively; g-1, g-2, first and second glumes; x, portion of rachis.

A second spikelet had three lemmas (fig. 2). The lowermost was empty, the second was fertile and normal, and the third subtended an abortive flower consisting of a one-styled ovary and a palea. As in the first spikelet, the paleas were similar to the lemmas in texture and form, although the abortive palea was smaller and its margins were inrolled. The other two spikelets showed the second bract or "glume" in different degrees of similarity to a normal lemma, but in both cases only one other bract was present below. In all the spikelets the cup below the position of normal articulation was divided into two or, as in one case, three separate scales, and there was no distinct articulation (fig. 3).

The presence of a lemma-like structure in the position of one of the "glumes" in three of the abnormal spikelets, and the presence of three such structures and no "glumes" in one spikelet, presents a fair indication that the bracts which in the taxonomic literature have been called glumes are in

reality reduced sterile lemmas. The scales, which I have assumed to represent the cup, could then be considered as extremely reduced glumes. Such an interpretation of the rice spikelet brings the Oryzeae very close to the Phalarideae as suggested by Mrs. Arber (1934, p. 184). What the extra small scale in one spikelet represents is not clear. It may be another reduced lemma.

If we assume that the anomalies which have been described represent a true picture of the homologies of the bracts in the rice spikelet, a question occurs in reference to the interpretation proposed by Peterson and by Parodi. In two spikelets more than one lemma was observed to have in its axil a bract similar to it in shape and texture. That is, the extra florets were constructed like the single floret in a normal spikelet. Are these also to be considered the result of fusion of two flowers? If this is true, then it will be necessary to reconsider the spikelet in terms of that hypothesis. If each lemma on a given axis has another in its axil it is a strong indication that a branching system is involved. To regard the rice spikelet as an extremely reduced branching system of which the lemmas represent entire spikelets would indeed set the genus *Oryza* off as a group in which the spikelet differs in origin from that of other grasses, and would lend support to Parodi's suggestion that the Oryzeae constitute a separate subfamily (Parodi 1939).

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FURTHER POLLEN STUDIES OF PEAT BOGS ON THE PACIFIC COAST OF OREGON AND WASHINGTON¹

HENRY P. HANSEN

INTRODUCTION

The moist climate of the Pacific Coast of Oregon and Washington and the progression of a post-Pleistocene marine cycle of a submergent shoreline has resulted in the formation of many freshwater ponds and subsequent hydrarch succession forming peat deposits. Many stages of hydrarch succession are to be found, from those in recently formed sand-dune lakes, supporting early submerged seres, to mature bogs covered with forests. This area lies beyond the limits of Pleistocene glaciation, but this geologic event has apparently been indirectly responsible for conditions favoring organic sedimentation during postglacial times. The nourishment of the continental ice sheet caused a lowering of sea level, which permitted down-cutting of streams emptying into the ocean. During deglaciation raising of sea level drowned the valley mouths of streams for many miles inland (Fenneman 1931). The marine cycle of submergence since then has resulted in the formation of several kinds of lakes, apparently with some chronological consistency. This is shown by the depth of the peat deposits, particularly on the margin of the larger lakes, formed in the blocked tributaries of the major streams. Ponding effected by movement of shore sand has taken place at later dates, and in fact is occurring continually along the coast, in the sand-dune zone. This includes embayment of small streams by spits and bars, blocking of small streams flowing parallel with the shore, and the formation of depressions by migrating sand dunes and possibly in some cases by deflation. Lakes formed in the tributaries of the larger streams at some distance from the ocean support the deepest peat deposits, and thus hold the probability of antedating those formed in the sand-dune zone. It is difficult to assign an age to these dune bogs, and an estimation must be based upon the depth of the peat and the average rate of deposition as determined by the average depth of the several profiles studied. Shifting of sand not only forms new depressions for potential hydrarch succession, but also buries bogs in varying stages of development. This is well shown by a stratum of fossil peat enclosed in terrace sands of a sea cliff near Newport, Oregon (Hansen & Allison 1942). The peat layer

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is overlain with 40 feet of sand which may be of either subaqueous or colian origin. A record of forest succession from pioneer forests of lodgepole pine to climax forests of spruce and hemlock is revealed by pollen analysis of the sediments. Thus it can be seen that the chronology of coastal peat bogs is indefinite, with many different ages represented and considerable overlapping of their periods of recorded time.

LOCATION AND CHARACTERISTICS OF THE BOGS

This study is concerned with a series of six peat profiles extending from Hauser, Oregon, north to Hoquiam, Washington, a distance of about 265 miles. In order, beginning at the south, the peat profiles are located near the following towns: Hauser, Newport, and Gearhart in Oregon; Ilwaco, Grayland, and Hoquiam in Washington. Those located near Hauser, Newport, Ilwaco, and Grayland have been formed in shallow sand dune lakes within a mile or two of the ocean. The bog at Gearhart has developed in a small stream valley, somewhat inland from the sand-dune zone, and is the deepest of the profiles. That near Hoquiam lies near sea level on the north side of Grays Harbor, just west of the mouth of the Hump Tulips River. It apparently owes its origin to a eustatic rise in sea level, causing drowning of stream mouths. Several feet of mud underlying the organic sediments suggest tideflat conditions for some time before freshwater hydrarch plant succession began. The existence of estuarine conditions in this area further suggests this possibility. The bogs vary in depth, the deepest being 7 m. at Gearhart; those at Hauser and Newport, 1.0 m.; near Ilwaco, 2.8 m.; at Grayland, 2.1 m.; and that near Hoquiam, 4.4 m. The bog at Gearhart is underlain with silt and clay, and all the others except at Hoquiam are underlain directly with sand. In sand-dune bogs, the organic sediments are sharply defined stratigraphically from the underlying sand, with no gradation into silt, clay, and limnic peat, such as usually occurs in inland bogs, both in the glaciated and unglaciated regions. This is due to the presence of only sand adjacent to the ponds, which prevents the income of fine silts and clays before organic sedimentation gets under way.

All the bogs are of the *Sphagnum* type. Portions of some of them have been drained and scalped for cranberry culture, which is an important industry along the coast of Oregon and Washington. The following species of plants are common to all the bogs; Labrador tea (*Ledum columbianum*), bog laurel (*Kalmia polifolia*), cranberry (*Vaccinium oxycoccus*), salal (*Gaultheria shallon*), sweet gale (*Myrica gale*), hardhack (*Spiraea douglasii*), skunk cabbage (*Lysichitum americanum*), cascara (*Rhamnus purshiana*), red alder (*Alnus rubra*), deer fern (*Struthiopteris spicant*), and yellow pond-lily (*Nymphaeozanthus polysepalus*). All bogs are in the climax stage and are being invaded by forest tree species. Generally, lodgepole pine

(*Pinus contorta*) is the pioneer and most abundant arboreal invader of the coast bogs, but occasionally Sitka spruce (*Picea sitchensis*) may be the initial invader. Other species that early encroach upon the climax bog are western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and occasionally Douglas fir (*Pseudotsuga taxifolia*). Along the southern half of the Oregon coast, Port Orford cedar (*Chamaecyparis lawsoniana*) is found with lodgepole pine. The determining factor in the order of arboreal bog invasion seems to be the availability and proximity of the several species. Lodgepole pine is usually the most abundant species in the sand-dune zone, and is usually preponderant as a seed disperser onto the bog surface. Observations show that either Sitka spruce or western hemlock may be the first invader if their propagules are available. On the Newport bog, hemlock is abundant on the eastern part, but not on the western edge. This is evidently due to the presence of hemlock forests adjacent to the eastern margin of the bog, while the forests to the west are composed of lodgepole pine and spruce. The prevailing westerly winds are a further factor favoring lodgepole invasion, as the forests located windward to the site of the bogs are usually composed of a preponderance of this species. The abundance of lodgepole pine on climax bogs is reflected in the pollen proportions of the upper horizons of peat, and tends to distort the recorded composition of the adjacent forests.

FORESTS OF ADJACENT AREAS

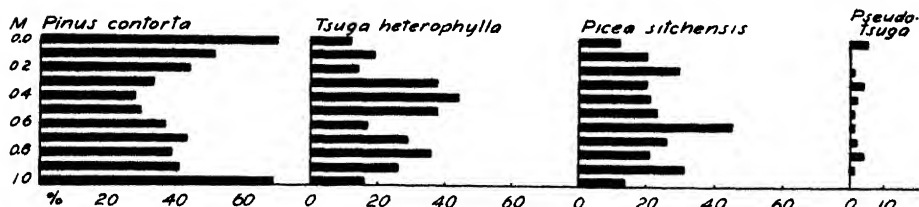
All six bogs lie within the Humid Transition life area (Bailey 1936). A narrow zone, several miles in width from the ocean to the Coast Range along the coast of Oregon and Washington, is spoken of as the fog belt because of the heavy precipitation. The mean annual rainfall at stations nearest the site of the sediments of this study is as follows: Newport, 67 inches; Astoria, 76 inches; and Aberdeen, Wash., 81 inches. Although the coastal strip is a part of the area designated as the hemlock-cedar climax of the Coast Forest (Weaver and Clements 1938), cedar is of minor importance in the forest complex. The principal dominants of the fog belt forests are lodgepole pine, Sitka spruce, and western hemlock. As the first is not a climax species, the coastal strip forests may be classified as the spruce-hemlock climax. Lodgepole pine is usually the first arboreal invader of sand dunes after they have been somewhat stabilized by lesser vegetation. Thickets of lodgepole near the ocean shore are low and rounded owing to sand-shear caused by the abrasive action of landward-borne sand. Individuals are much misshapen, and often resemble the Krummholz form of trees at timberline. Occasionally a specimen of spruce is found in the thickets of lodgepole, but hemlock has not been observed under these conditions. Farther inland, lodgepole assumes a tall, straight form and dense thickets serve as a windbreak for other species. Leeward to the pine zone, and mixed with it to some extent, are spruce and

hemlock. These species become progressively more abundant farther inland, lodgepole gradually thinning out because of its intolerance for shade. Still farther away from the ocean, Douglas fir enters the forest complex, while spruce becomes less abundant, gradually giving way to hemlock and Douglas fir. Hemlock in turn surrenders its predominance to Douglas fir in the Coast Range to the east. When the forests on the sand dunes are burned, lodgepole pine may regain its preponderance; or farther from the ocean Douglas fir often makes its appearance and become locally predominant until replaced by spruce and hemlock. Other forest tree species apparently within range of pollen dispersal to the site of the sediments are western white pine (*Pinus monticola*), lowland white fir (*Abies grandis*), noble fir (*A. nobilis*), and silver fir (*A. amabilis*). The most important broadleaf species are red alder, bigleaf maple (*Acer macrophyllum*), and black cottonwood (*Populus trichocarpa*).

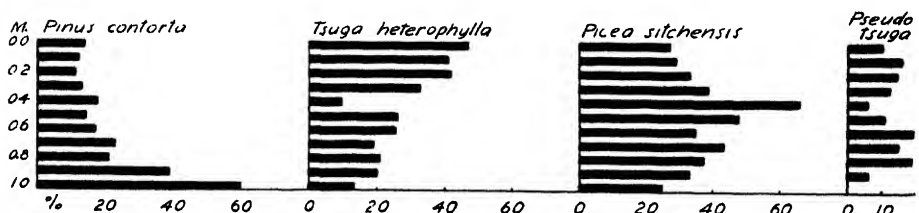
FOREST SUCCESSION

Although the general forest physiognomy of the coastal strip in which the peat profiles are situated is more or less homogeneous, the recorded forest succession for the period represented varies somewhat in the several areas. This may be due to the different ages of the bogs, the varying forest composition and stages of succession during initial sedimentation, the different trends of forest succession because of differences in topography, varying degrees and periods of sand movement, and the position of the bog in relation to sand dunes, the ocean, prevailing winds, and the adjacent forests. Perhaps the most important factor that influences forest succession and tends to interrupt the normal succession along the Oregon and Washington coast is sand-dune movement. Periodic shifting of dunes may bury forests in various stages of succession, from the pioneer forests of lodgepole pine to more mature forests of spruce and hemlock. The first are more prone to be destroyed because of their proximity to the ocean and their establishment on less stabilized soil than the climax forest. The destruction of the lodgepole forests is perhaps more readily reflected in the pollen profiles than the climax forests, because the bogs usually lie leeward to the pine zone. Thus, fluctuations in the pollen profiles of the several species, when contrary with one another, or one group with another, may denote relative rather than actual changes of the recorded species. One can assume that fluctuations in pollen profiles of coast bogs are probably more often a result of changes in the actual abundance of lodgepole pine, rather than in spruce or hemlock. The location of pine forests, largely windward to the bogs, and the greater amount of pollen produced by this species undoubtedly cause over-representation by its pollen. The maturation of lodgepole pine at a much earlier age than the other species gives it more maneuverability in an unstabilized dune

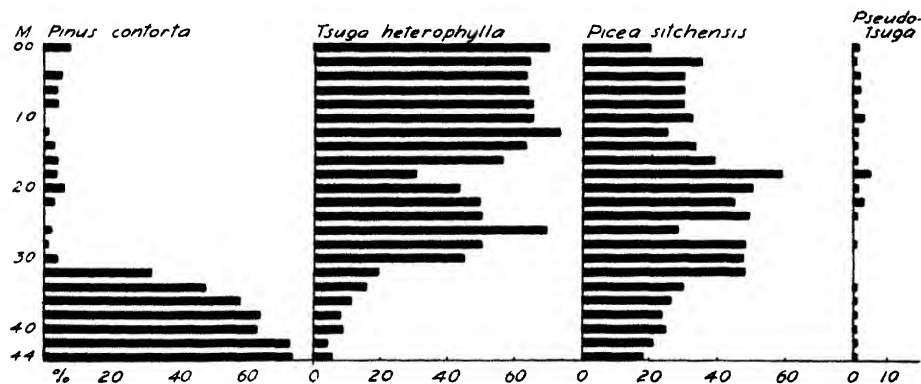
area. Not only is it better adapted to invade newly formed dunes, but it is also better able as a forest to recover after, or even during, its destruction by burying or fire than spruce or hemlock, which require many years before attaining seed-bearing age. Spruce and hemlock forests producing relatively



1



2



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FIG. 1. Pollen profiles, Newport, Oregon. FIG. 2. Pollen profiles, Hauser, Oregon. FIG. 3. Pollen profiles, Hoquiam, Washington.

less pollen and lying largely leeward to the bogs are probably generally under-represented in the pollen profiles.

The similarity in the composition of the peat of the six profiles suggests about the same rate of deposition. The profile near Gearhart, being the deep-

est, would also represent the greatest period of time for its deposition. Its location and method of formation also indicate a greater possible age, and it is the only profile that seems to hold the potentiality of representing most or all of postglacial time. The trends of adjacent forest succession as recorded in the profile seem to substantiate this theory.

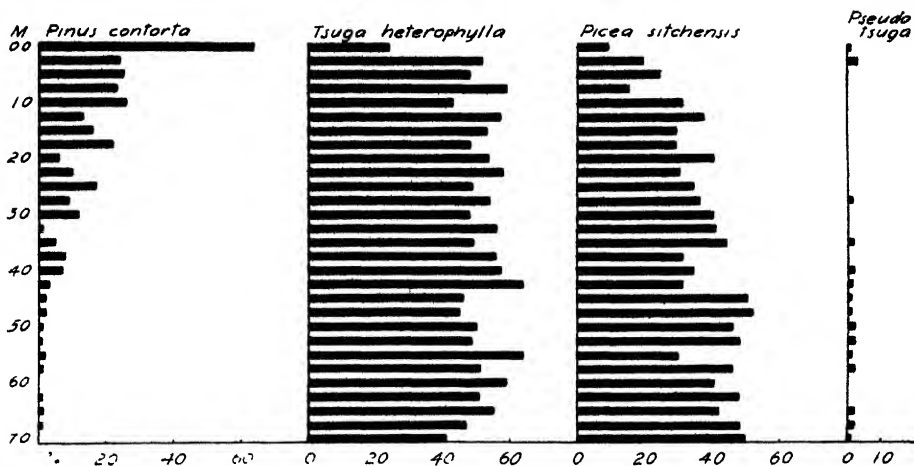
Three of the profiles, those at Newport, Hauser, and Hoquiam reveal a preponderance of lodgepole pine in the lower levels (figs. 1, 2, 3). This is also shown in two sand-dune bogs farther south on the Oregon coast, near Bandon and Marshfield (Hansen 1943). Lodgepole pine has generally been the pioneer postglacial invader in the Pacific Northwest, especially in the glaciated region. In these areas, however, forest succession started anew as the ice retreated, whereas the coastal strip of Oregon and Washington was probably forested during the glacial period with the present day species. In the Hauser profile lodgepole pine is recorded as having gradually declined from 60 per cent at the bottom to 14 per cent at the top. At Newport, lodgepole declines from its maximum of 69 per cent at the bottom to its minimum of 28 per cent at 0.4 m., and then increases to 66 per cent at the surface. The resurgence of lodgepole at the surface reflects its invasion of the bog and its abundance in sandy areas west of the bog. Lodgepole is not so abundant adjacent to the Hauser bog, and the surface has been scalped for cranberry culture, with the elimination of much of the source for its pollen.

In the Hoquiam profile, lodgepole is recorded to its maximum of 74 per cent at the lowest horizon, from which level it abruptly declines to only 4 per cent at 3 m., and then fluctuates between nothing and 8 per cent to the top. There is less dune area in this vicinity, much of the adjacent region consisting of low swampy ground forested with hardwood species, and gravelly knolls covered with climax forest.

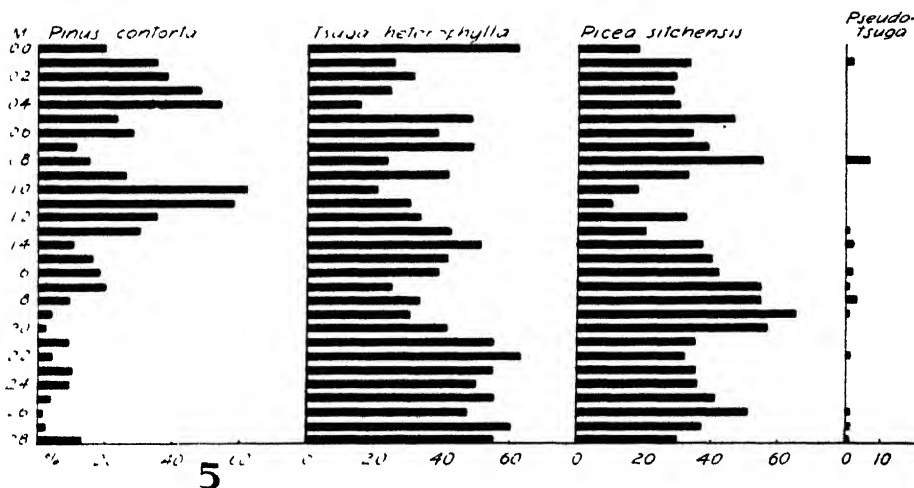
In the other three profiles, lodgepole is recorded to less than 15 per cent at the lowest horizons, but shows slightly different trends upward in the profiles. At Gearhart it shows a general increase upward, to reach its maximum of 63 per cent at the surface (fig. 4). The accelerated increase in more recent time marks its invasion of the bog. Apparently the Gearhart bog had its inception when the adjacent forests existed in the climax stage. Since that time, the major trend of pine has been its more recent encroachment upon the bog. A similar situation apparently was present in the vicinity of a 12 m. profile farther south, near Florence, Oregon (Hansen 1941). Here, in an area inland from the sand-dune zone, climax forests of spruce and hemlock also existed when sedimentation was begun. In the Ilwaco profile, pine is revealed as having fluctuated considerably during the period represented (fig. 5). It

Explanation of figures 4-6

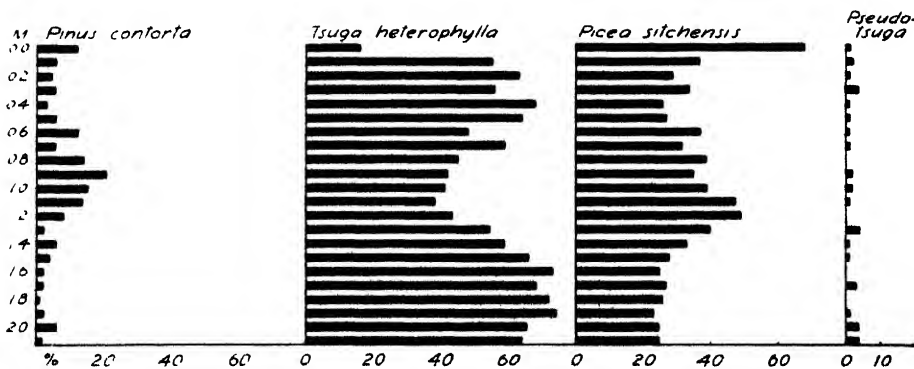
FIG. 4. Pollen profiles, Gearhart, Oregon. FIG. 5. Pollen profiles, Ilwaco, Washington.
FIG. 6. Pollen profiles, Grayland, Washington.



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is recorded as 13 per cent at the bottom, fluctuates between 1 and 20 per cent to 1.4 m., and sharply increases to its maximum of 62 per cent at 1 m. It then abruptly declines to 11 per cent at 0.7 m., followed by a marked increase to 54 per cent at 0.4 m., and then a final decline to 20 per cent at the top. These marked trends evidently record extensive and periodic dune movement, burying forests of lodgepole on one hand, and providing new areas for its invasion on the other. The Ilwaco profile is located in the most extensive dune area of the six bogs, at the mouth of the Columbia River. Here the strong winds follow up the Columbia, causing movement of sand from both the west and the south. The vast Long Beach spit extends for 15 miles to the north. The presence of large bog areas in this region has probably been responsible also for lodgepole pine fluctuation. Invasion of bogs occurred at various times, as they reached the climax stage, and such invasions are undoubtedly represented in the pollen profiles by an increase in pine pollen. The presence of charred peat at 1.0 m. suggests that fire may also have been a factor in the abrupt increase of pine to its maximum at this horizon. In the Grayland bog pine is recorded as only 2 per cent at the lowest level, from which point it increases to its maximum of 21 per cent at 0.9 m. (fig. 6). It declines to 6 per cent at 0.1 m. and then increases to 12 per cent at the top. The latter increase reflects its limited encroachment upon the bog in recent time. Both the Ilwaco and Grayland bogs apparently had their initiation when climax forests existed in their vicinity.

The climax species, spruce and hemlock, show considerable fluctuation in all profiles. Most of these fluctuations are opposed to each other, rather than to that of pine, because the latter reveals many trends that are neither opposite nor similar to those of hemlock and spruce, either collectively or as to individual species. An increase in spruce and hemlock from the bottom to half-way up in the profile is contrary to pine decrease. A continued sharp rise in spruce to 66 per cent at 0.4 m., however, is contemporaneous with a decline of hemlock, and pine shows a slight increase to this same level (fig. 2). A sharp reversal of trends for spruce and hemlock from this horizon to the surface denotes continued competition between these species, as lodgepole remains constant. In the Newport profile, spruce and hemlock trends are opposed at every level except from the bottom to that immediately above (fig. 1). The trend of lodgepole pine apparently has been independent throughout the entire period represented. In the Gearhart bog, again the recorded trends of spruce and hemlock have been largely contrary to each other, with the latter predominant throughout, while lodgepole reflects only its invasion of the bog itself (fig. 4). The Ilwaco profile discloses several short period fluctuations of all three species (fig. 5). Some involve spruce and hemlock fluctuating oppositely to lodgepole, others concern contrary trends of spruce and hemlock, and still others denote fluctuations of lodgepole con-

trary to either spruce or hemlock. The major fluctuations of pine suggest accelerated dune movement, first burying pine forests, then supporting pine invasion, and finally replacement of pine with spruce and hemlock as stabilization of edaphic conditions progressed. The occurrence of charred peat at 1 m., the level of pine maximum, suggests the possibility of fire as having been instrumental in the development of this trend. The pollen-bearing sediments at Grayland also were apparently inaugurated when the adjacent forests existed in the climax stage (fig. 6). The trends of spruce are largely the converse of hemlock, whereas those of lodgepole seem to be independent. From its initial predominance, hemlock declines whereas spruce increases to 1.1 m., then their trends are reversed to the horizon immediately below the surface, where hemlock again decreases and spruce increases to the top, the latter being preponderant. There are several possible events suggested by these trends. Fire may have destroyed the hemlock forests, increasing the relative abundance of spruce and pine. Sand dune movement may have permitted an increase in spruce and pine. A third possibility for spruce expansion is its invasion of other climax bog areas in the vicinity. The resurgence of hemlock from 1.1 m. to immediately below the surface suggests normal forest succession. The final increase of spruce at the expense of hemlock may mark the invasion of spruce on the bog. In the Hoquiam sediments, the trends of spruce and hemlock are opposed throughout the profile. Hemlock reveals an increase from 6 per cent at the bottom to 71 per cent at 2.6 m., with spruce remaining constant. Then with several minor fluctuations, hemlock attains its maximum of 73 per cent at 1.2 m. and spruce declines to 25 per cent at the same level, and then both species remain generally constant to the top (fig. 3). Dune movement has apparently played a minor role in forest succession in this region, the expansion of lodgepole pine to 21 per cent at 0.9 m. after its initial decline being the only period indicating unstabilized edaphic conditions.

Other forest tree species are only sparsely and sporadically represented. In the Hauser profile, Douglas fir is recorded as high as 20 per cent, and closely follows the trends of hemlock, while in the others it has a limited representation and not at every horizon. The bogs are located windward to the Douglas fir forests of the Coast Range. Other species recorded are western white pine, lowland white fir, noble fir, and silver fir. A non-indicator of adjacent forest succession consistently represented by its pollen in appreciable proportions is red alder. Species confined largely to the bogs, which provide abundant pollen at various levels, are myrtle, willow, maple, several species of *Ericaceae*, sedge, yellow pond-lily, and cattail. The pollen proportions of these species mark the development of hydrarch succession from submerged to climax seres.

There seems to be little evidence for climatic trends in the pollen profiles of the several species represented. There probably have been slight climatic changes during the post-Pleistocene along the coast of Oregon and Washington, because of the moderating influence of the ocean. The principal factor influencing forest succession has probably been sand movement. The inland movement of sand modifies and retards the rate of forest succession, and in some cases terminates it by burying forests. The formation of spits and bars and the building up of the beach provide primary areas for succession. Periods of extensive sand movement may reflect climatic changes farther inland, bringing about increased wind velocity for periods of time sufficient to cause considerable shifting of sand. Eustatic changes in sea level may also be reflected by increased sand movement. Emergence of land may have provided more eolian material and new areas suitable for primary forest succession. There apparently are many complex variables involved in initiating sand movement and the forest succession which it controls to a large extent. Most of these seem to be intangible as far as their application to interpretation of pollen profiles is concerned.

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STUDIES ON AMERICAN HEPATICAE—V. TWO NOMENCLATURAL CHANGES IN CERATOLEJEUNEA

MARGARET FULFORD

The following new species and new combination have resulted from a recent study of the genus *Ceratolejeunea*:

Ceratolejeunea grandibracteolata Fulford, sp. nov. (*Ceratolejeunea subserrata* Spruce, Hep. Spruc. (not *L. (Cerato-Lejeunea) variabilis* var. *subserrata* Spruce, Trans. & Proc. Bot. Soc. [Edinburgh] 15: 207. 1884).

Caules ad 2.5 cm. longi, 1.2 mm. lati, rufobrunnei; folia grandia, oblonga, apice lato, rotundato, integra vel leviter dentata; dente apicali lobuli brevi, curvo, obtuse acuminato; utriculis saepe praesentibus; cellulae 20–24 μ , trigoniis conspicuis, ocellis geminatis, basilaribus; amphigastria grandia, orbicularia: dioica; bractae femineae lobus late ovatus, lobulo explanato, oblongo, margine integro; bracteolus connatus, late ovatus, bifidus ad partem tertiam longitudinis, margine integro; perianthium emergens, cornibus angustis, brevibus, divaricatis: rami masculi non visi.

Ceratolejeunea flagelliformis (Steph.) Fulford, comb. nov. (*Ceratolejeunea spinosa* var. *flagelliformis* Stephani, Hedwigia 34: 238. 1895. *Lejeunea (Ceratolejeunea) flagelliformis* Stephani, Hepat. in Duss, Muscinées Ant. Franç. 13. 1903 The characters of the perianth, which has only recently been discovered, at once set these plants apart from any of the other American species.

UNIVERSITY OF CINCINNATI

AND

THE NEW YORK BOTANICAL GARDEN

SPORELINGS AND VEGETATIVE REPRODUCTION IN THE GENUS *CERATOLEJEUNEA**

MARGARET FULFORD

A taxonomic study of nineteen American species of the hepatic genus *Ceratolejeunea*, just completed,¹ has brought to light several stages of sporeling development in eleven of the American species and one from Java, and examples of vegetative reproduction in eight species. It is, I believe, the first time that sporelings of this genus have been identified, and also the first time that so large a number of sporelings of a genus could be compared. Although the structures of vegetative reproduction have been mentioned in the literature they were never discussed in any detail.

1. SPORELINGS

In a recent paper² in which several additional types of sporelings were described in the family *Lejeuneaceae*, the question whether the pattern of development was uniform for all of the species had to remain unanswered, since at that time, sporelings of only one species in any of the genera under discussion had been observed. There was also little information on the degree of variation that was to be expected in the numerous sporelings produced by one or several plants of a given species.

It is now fairly certain that the sporeling described and figured by Goebel³ as belonging to an unknown South American genus, as well as the one described and figured by the writer,⁴ as representing a further development of the type discussed by Goebel, belong to the genus *Ceratolejeunea*. These two clearly typify the basic pattern of sporeling development at its best in the genus. It may well be designated the *Ceratolejeunea* type.

The sporeling of the genus *Ceratolejeunea* (except for *C. guianensis*), is made up of a unistratose thalloid portion of two distinct stages: a filament two cells broad and four cells long which develops within the old stretched exospore; and a broader, secondary thallus four cells broad and of indefinite length. The leafy axis develops at the end of this secondary thallus.

* This work was made possible through a Marshall A. Howe Memorial Fellowship given by Mrs. Elon Huntington Hooker to the New York Botanical Garden, for the summer of 1943.

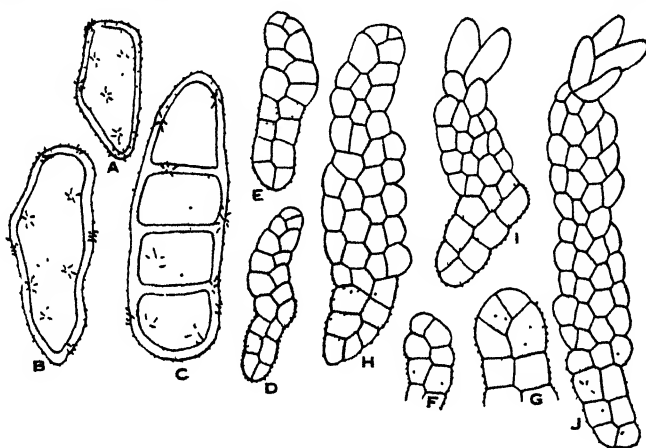
¹ Fulford, M. Studies on American Hepaticae—VI. *Ceratolejeunea*. To be published in *Brittonia*.

² ———. Development of sporelings in the *Lejeuneaceae*. *Bull. Torrey Club* 68: 627-633. f. 1-4. 1942.

³ Goebel, K. *Organographie der Pflanzen* 2: 907, fig. 972. 1930.

⁴ Fulford, M. Development of sporelings in the *Lejeuneaceae*. *Bull. Torrey Club* 68: p. 631. fig. 3. 1942.

As in the other genera of the *Lejeuneaceae* which I have observed, the spore elongates and becomes chlorophyllose before it is shed from the capsule. Just before the capsule opens the spore is green, two or three times as long as broad, and the wall is thick and hyaline. The exospore is papillose and, in addition, has a scattered pattern of "rosettes" composed of coarser lines of deposition, as is seen in figure A. This spore continues to elongate (fig. B), and very soon, through the formation of a series of three walls at right angles to the long axis, contains four cells (see fig. C). In most instances this division takes place after the spore is discharged. During the elongation of the spore the exospore wall increases in extent, for the distance between papillae increases and the rays of the "rosettes" spread (fig. C).



FIGS. A-J. Stages in the development of the leafy plant from the spore, in the genus *Ceratolejeunea*. FIGS. A-C, spores at about the time they are shed from the capsule. FIGS. D-E, The eight-celled thallus within the old exospore with its characteristic markings, and the partly developed secondary thallus (without markings) developed from the apical cell with two cutting faces. FIGS. F-G, Initiation of the apical cell with two cutting faces from a cell at the end of the thallus within the exospore. FIGS. H-J, Stages in the development of the sporling including the early stages of the leafy shoot. Figures A-C, $\times 400$; D-J, $\times 200$.

These latter tend to become less conspicuous with the increase in the size of the protonema, and in its later stages are usually not noticeable (see figs. D-J).

Apparently the next stage is the formation of a wall more or less parallel to the long axis of the spore, in each of the four cells, so that an eight-celled thallus is formed. It is, of course, two cells broad and four cells long. This eight-celled filament can always be distinguished because of its papillose wall, the exospore. Sporlings which had reached this stage but had not developed beyond it could not be found.

The next stage was one in which an apical cell with two cutting faces had already developed from a cell of the eight-celled thallus. Figures F and G

show the initiation of such an apical cell. Through the activities of this apical cell two rows of segments are cut off, resulting in the formation of a secondary thallus, clearly distinguished by the smooth walls of its cells (figs. D, E).

Each of the segments cut off from the apical cell soon divides again by a wall more or less parallel to the long axis of the thallus; and in this way the secondary thallus becomes four cells broad. Figure H illustrates development to this point. The thallus within the old exospore is papillose; the remainder, the secondary thallus, is fully developed below, four cells broad, and near its tip shows several segments not yet divided, and the apical cell.

After a variable number of segments have been cut off, the apical cell becomes transformed into an apical cell with three cutting faces. This gives rise directly to a leafy shoot with no intermediate stages (see figures I and J).

The first leaves formed are of the primary type, small, ovate-lanceolate, and plane. These are followed by the larger, juvenile leaves with large water-sacs, which are usually accompanied by underleaves. The details of the leafy plants of individual species are discussed below.

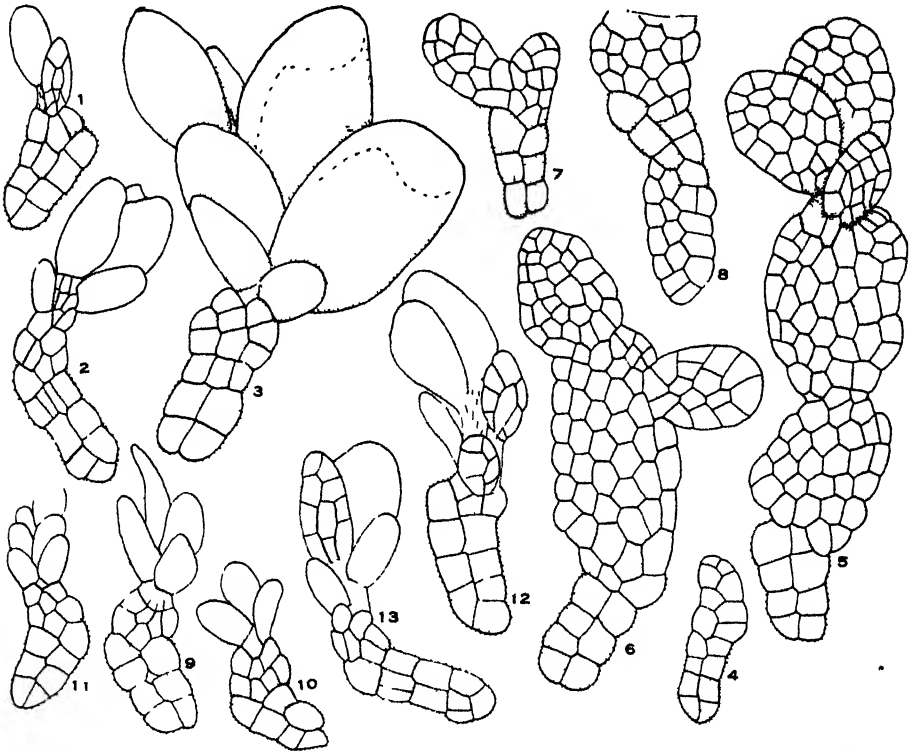
The above is a brief résumé of what I consider to be the pattern of development of the sporcling of the genus *Ceratolejeunea* (except for *C. guianensis*). Of course, many of the sporclings do not conform to this pattern in all of its detail, and I have attempted to illustrate the deviations in the discussion of individual species. This method tends to emphasize the exceptions rather than the more usual pattern of development, since the majority of the figures are examples of the deviations which were observed, while the majority of the sporclings conform to the basic pattern.

The grouping of the species is here based on the type of horns of the perianth, and the three species which follow have perianths with large, bulbous horns. However, *C. malleigera* is an aberrant species, since only two instead of the customary four horns are produced.

C. SPINOSA (G.) Steph. (Figures 1-3) None of the few sporclings which were found had the broad, secondary thallus developed to any extent; in fact, in figures 1 and 2 it is scarcely suggested and in figure 3 is very poorly developed. The formation of additional walls in some of the cells of the thallus within the exospore, so that it becomes more than two cells broad as is shown in figure 2, is not uncommon. This figure also suggests the formation of a second apical cell and therefore a growing point, at the other end of the thallus. Spores in unopened capsules were too immature for detail of the spore wall, but they were papillose and the "rosette" pattern was suggested. Figure 3 illustrates a plant in which both primary and juvenile leaves had developed. It is curious that the three leaves on the left side of the stem are of the primary type, while two of the three on the right are of the juvenile

type, yet all of them developed from alternating segments of the same apical cell. No underleaves were observed.

C. MALLEIGERA (Spr.) Steph. (Figures 4-8.) These sporelings were among the fruiting plants of the original and only collection of the species. The eight-celled stage within the exospore was quite uniform in its development throughout, except that occasionally only six cells were formed. Development proceeds in the usual fashion (see figure 4 and the lower part of figure 8), except that the outer cell of the pair formed by each segment usually divides

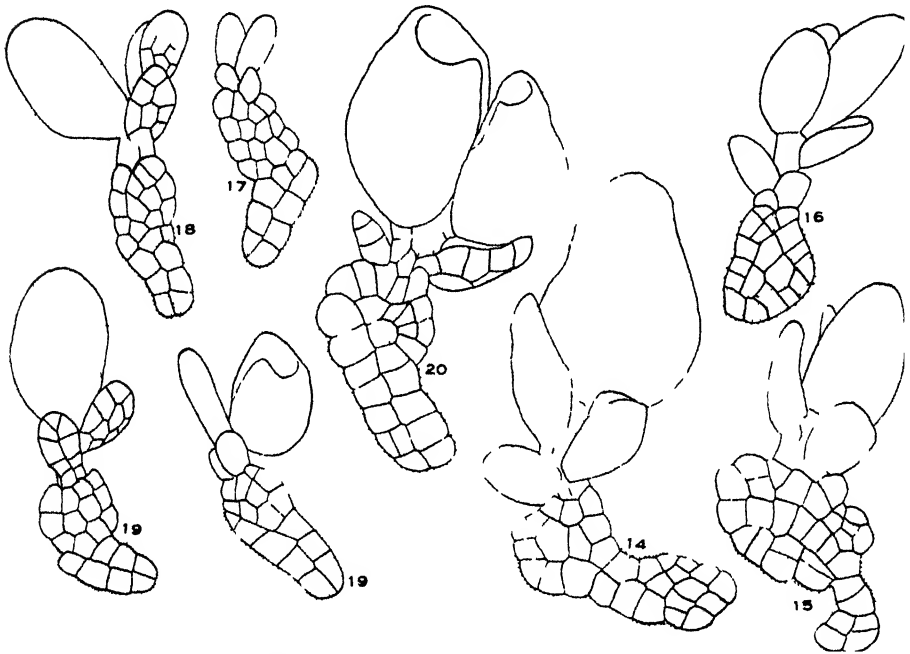


FIGS. 1-3. *C. spinosa* (G.) Steph. Figures 1-2 from Suringar, West Indies; figure 3 from Brentel, St. Kitts, the original. FIGS. 4-8. *C. malleigera* (Spr.) Steph., from the original, Bolivia. FIGS. 9-13. *C. plumula* (Spr.) Steph. Figures 9-10 from Duss 44, Gudeloupe, figures 11-13 from Spruce, Brasil. All $\times 200$.

again so that the secondary thallus is six cells broad throughout most of its length. This development can be followed in detail in the upper part of figure 6. A striking example of a broad secondary thallus grown out from each end of the eight-celled thallus is shown in figure 8. Figure 5 illustrates the only example of the formation of leaves on sporelings of this species. They are all of the primary type. No underleaves are evident. Here also, growth of the broad secondary thallus was restricted for a time, then pro-

gressed after the usual pattern. Branching of the secondary thallus is not uncommon (see figures 6 and 7); the branch arises from a marginal cell.

The presence of a secondary thallus broader than that customary in the genus raises the question of the taxonomic position of the species, especially since the species is also unusual in that there are only two instead of four horns on the perianth, and the ocelli of the leaves are no larger than the leaf cells and are numerous and scattered throughout the leaf. In most of the species the ocelli are large, and from one to several in a basal position, or they form a nerve. Even with the differences mentioned above this species



FIGS. 14-16. *C. flagelliformis* (Steph.) Fulford. Figures 14-15 from *Kians*, Puerto Rico; figure 16 from *Duss 385*, Martinique. FIGS. 17-20 *Ceratolejeunea* sp. from the Mitten Herbarium, collected in Java. All $\times 200$.

certainly resembles species of *Ceratolejeunea*, but its taxonomic position as a member of the genus might be questioned.

(*C. PLUMULA* (Spr.) Steph. (Figures 9-13.) Spores in the immature capsule were densely papillose, and also suggested the "rosette" pattern of markings, but no free spores in the early stages of sporeling development were found. The older sporelings suggest very strongly those of *C. spinosa* described above. The thallus within the old exospore is clearly delimited, although more than eight cells are sometimes present (see figure 13). The broad secondary thallus is extremely limited and sometimes scarcely developed, as was the case in *C. spinosa* (compare figures 9 and 10 with figure 12).

The next two species are characterized by having the horns of the perianth extremely long, slender, and terete.

C. FLAGELLIFORMIS (Steph.) Fulford. (Figures 14–16.) Not more than half a dozen sporelings were seen; all of them were irregular in their development and did not conform well with the general pattern. In all examples the thallus within the exospore was very irregularly developed. The irregular cell plate formed within the exospore shown in figures 14 and 15 may well have developed from an eight-celled thallus, since these cells showed a remarkable capacity to divide; there is evidence of more than one growing point; and only a part of each thallus in question is covered by the old exospore. It is possible also that the development of the thallus shown in figure 16 could have come about in the same way. A rudimentary secondary thallus is to be seen in figures 14 and 15 but none is apparent in figure 16. The leafy stem develops in the usual manner.

CERATOLEJEUNEA sp. (Figures 17–20.) This unnamed material, collected in Java, is in the Mitten Herbarium at the New York Botanical Garden. The species is very similar to *C. flagelliformis*. The leaves have a “nerve” of ocelli. All of the many sporelings observed in this material exhibited the usual pattern of development (figs. 17–19). Figure 20 shows a plant with more than the usual number of cells in the thallus covered by the exospore, and with a secondary thallus broader than in the other specimens. This thallus suggests the irregular development which was seen in *C. flagelliformis*.

The following species belong to that large group within the genus in which the perianth exhibits no striking characteristics. The horns are of characteristic length or are developed as short knobs.

C. BREVINERVIS (Spr.) Evans. (Figures 21, 22.) Many examples of the early stages of development were observed, and the pattern conforms to that described earlier. Figures 21 and 22 present the usual picture. The secondary thallus is poorly developed in figure 22 but is somewhat larger in some of the examples not shown here. The leafy axis presents a difficult problem. At its base it bears a pair of primary leaves followed by a pair of larger juvenile leaves with their large water-sacs. These are followed on the left side of the stem by another primary leaf and then a juvenile leaf, but on the right side of the stem, above the first juvenile leaf are two leaves with small ventral lobes, more or less intermediate in form between primary and juvenile leaves, followed by another juvenile leaf. All of these leaves have developed from segments of the same apical cell. An underleaf occurs on the upper part of the stem.

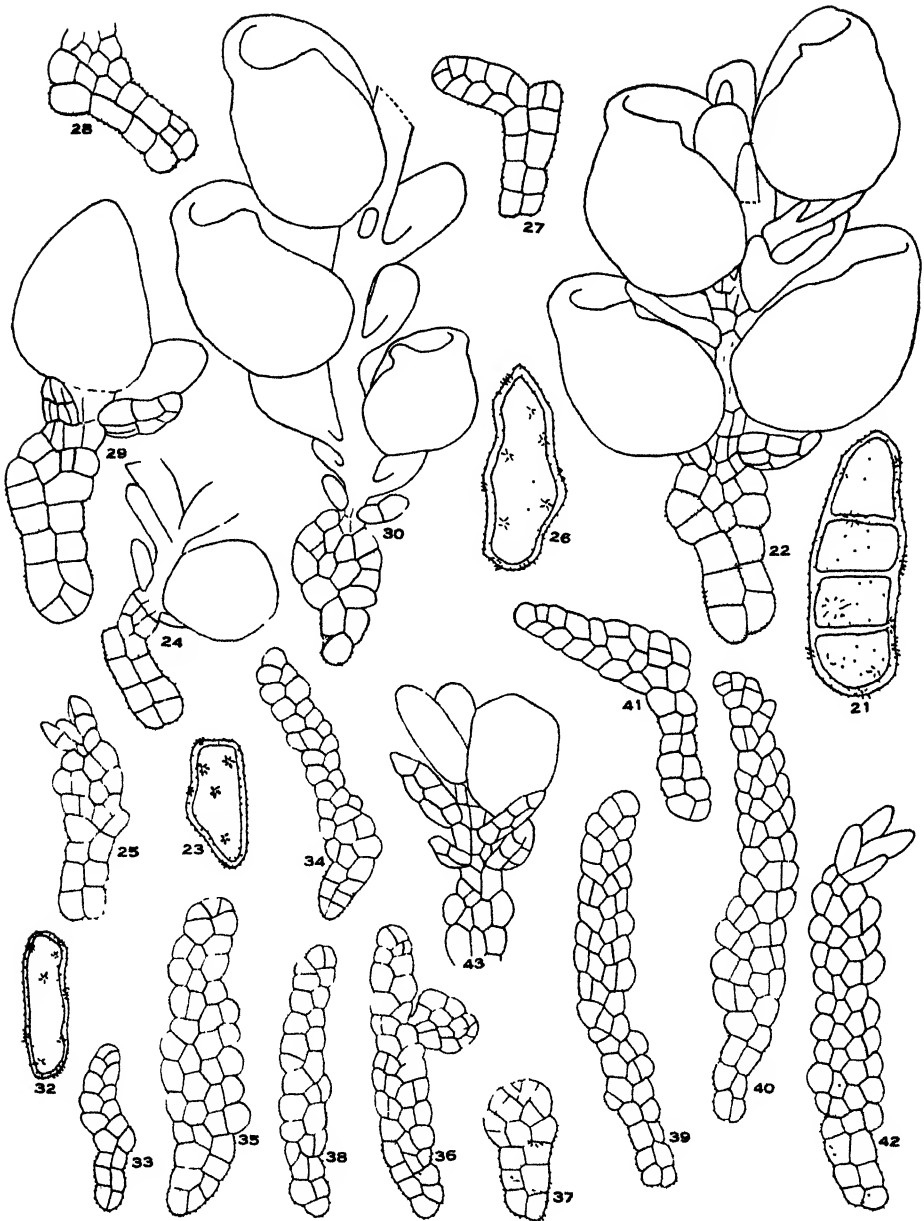
C. MARITIMA (Spr.) Steph. (Figures 23, 24.) These figures were drawn from plants collected by Spruce along the Amazon. They are from the spores of plants of the variant in which the leaf usually has a conspicuous "nerve" of large ocelli, and in which spherical lobules are for the most part absent. Plants of this character compose only one of several of the variants of the species which occur in tropical America.⁵ Spores from within capsules not quite mature were papillose and showed, in addition, the "rosette" pattern of supplementary thickenings. The advanced sporelings were in a poor state of preservation but all of them showed the characteristic eight-celled thallus within the exospore, and also a poorly developed secondary thallus. Figure 24 is characteristic of the group.

C. GRANDIBRACTEOLATA Fulford. Figure 25 is from material collected by Spruce along the Rio Negro in Brazil. It is the only example of a sporeling of this species which was sufficiently well preserved to be illustrated. It conforms to the general pattern, with eight cells in the exospore, one end-cell of which has given rise to an apical cell with two cutting faces. This in turn gave rise to segments which have formed the secondary thallus four cells broad. After several segmentations the growth of the thallus was terminated through the development of the apical cell with three cutting faces which produced the leafy plant.

C. MEGALOPHYSA (Spr.) Steph. (Figures 26-30.) This species also exhibits the usual range of deviation in the various stages of the development of the sporeling. The spores are similar to those of the other species in shape and wall-sculpturing. Figure 28 shows supplementary growth and the probable initiation of a second apical cell during the eight-celled stage. A thallus in which an apical cell has developed at each end is shown in figure 29. In figure 30 the thallus which was developed in the old exospore is poorly represented, perhaps it never was developed in full, and the secondary thallus is short. This leafy plant also has an assortment of primary and juvenile leaves on both sides of the stem. Underleaves are absent.

C. CUBENSIS (Mont.) Schiffner. (Figures 32-36.) Large numbers of sporelings in the various earlier stages of development are present in the material but none of them had developed leafy shoots. The spore at about the time that it is shed from the capsule is similar to those of the other species, green, elongate, papillose, and with supplementary markings in the "rosette" pattern (see figure 32). The thallus developed within the exospore is uniform, i.e. always of eight cells, and rarely was a variation observed. The apical cell with two cutting faces forms the usual secondary thallus two cells broad

⁵ Fulford, M. Studies on American Hepaticae—VI. *Ceratolejeunea*. To be published in Brittonia.



FIGS. 21-22. *C. brevinnervis* (Spr.) Evans, from Evans 232, Jamaica. FIGS. 23-24. *C. maritima* (Spr.) Steph. from Spruce, Amazon. FIG. 25. *C. grandibractcolata* Fulford, from Spruce, Brasil. FIGS. 26-30. *C. megalophysa* (Spr.) Steph. Figure 26 from E. G. Britton, D. Coker, Rowland, Trinidad; figures 27-30 from Smith, British Guiana. FIGS. 32-36. *C. cubensis* (Mont.) Schiffn. Figure 32 from Mosén, Brasil; figures 33-34 from Br. León & Clement 5561, Cuba; figures 35, 36 from Ramon de la Sagra, Cuba. FIGS. 37-43. *C. rubiginosa* Steph. from Wright, Cuba, the original. Spores, $\times 400$; sporophytes, $\times 200$.

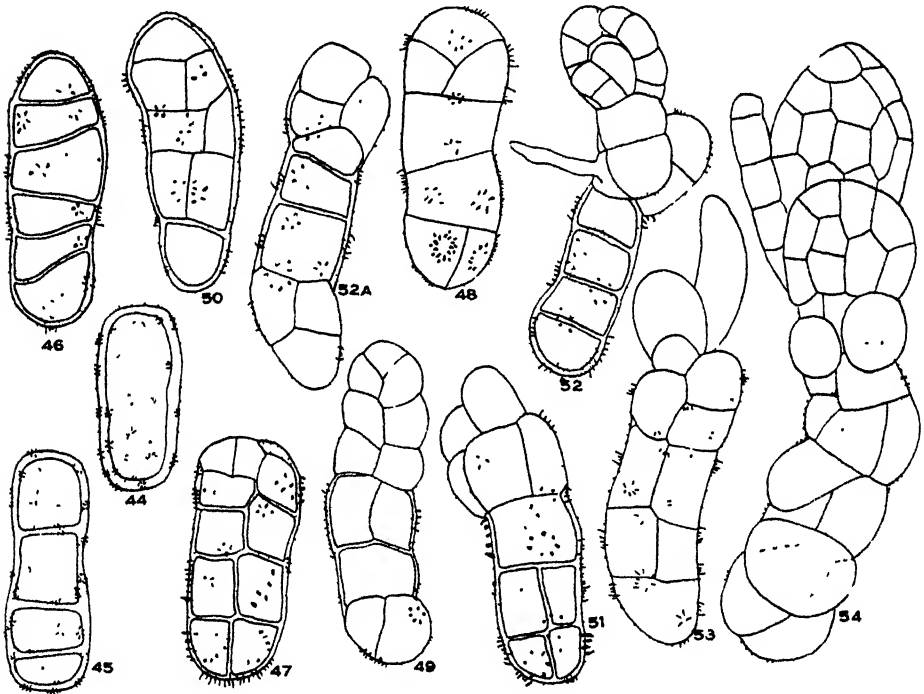
(fig. 33), which very soon through additional divisions of the segments becomes four cells broad (see figures 34–36). Branches are sometimes formed from marginal cells of the secondary thallus, as is indicated in figure 36.

C. RUBIGINOSA Steph. (Figures 37–43.) All of the drawings were from sporelings in the original material, collected by Wright in Cuba. This species closely resembles *C. cubensis* in habit and the sporelings also are very similar. They were present in great numbers and were remarkably regular in development. However, some of the usual deviations do occur; for example, less than eight cells in the exospore appear in figure 38, and an apical cell at each end of the eight-celled thallus is seen in figure 41. For the most part, the markings of the exospore are faint and scattered, but even the “rosette” pattern is present on some of the younger sporelings, as seen in figure 37. The first leaves formed on the shoot are of the primary type (figs. 42, 43), and are followed by the characteristic juvenile leaves (fig. 43).

C. GUIANENSIS (N. & M.) Steph. (Figures 44–54.) The sporelings of this species differ markedly from those described above for the other species of the genus. In addition, even the spores from one capsule may show a curious range of variation in their patterns of development. The spores are green, elongate, and have the markings characteristic of the genus at the time that they are shed from the capsule (fig. 44). After this a series of cross walls is formed, cutting off four cells as in the other species (fig. 45), or a variable larger number (fig. 46). It appears that either of two types of development may then take place in these filaments. Either a plate of cells two cells broad, four cells long, and one layer of cells thick may develop (fig. 47), as in the other species, or the filament may divide irregularly so that a slender, cylindrical mass of cells is formed (see fig. 50). Figures 47 and 50 were made from sporelings from the same capsule. In addition, a few of the sporelings had developed an apical cell with two cutting faces from one end of the thallus within the old exospore (figs. 48, 49), and in one of them a secondary thallus several cells long had been formed (fig. 49). None of the more mature sporelings which were observed showed an indication of such a secondary thallus. All of these older sporelings (25 or more from several capsules were studied), were of the types shown in figures 53 and 54, and those on which several primary leaves were well developed were similar to that illustrated in figure 54. Here a slender, cylindrical mass of cells develops within the old exospore and at one end of this the leafy shoot is formed. Figures 51–52a illustrate variations in which part of the thallus within the exospore is one layer of cells thick and part is several cells thick. They suggest transitional stages between the two modes of development. The thallus shown in figure 53 must have originated through earlier stages such as those illustrated in figures 45 and 47; while a thallus of the sort shown in figure 54 suggests earlier

stages like those illustrated by figures 46 and 50. The sporelings illustrated in figures 46, 47, 49, 50, 51, 52 and 52a came from one capsule. Here, the variations are certainly internal in origin, rather than the result of the influence of the environment. The material suggests that the cylindrical type of thallus is the final result of development within the old exospore, and that it may be arrived at through either of several patterns of development.

The discovery of a sporeling pattern in *C. guianensis* totally different from any yet observed in any other species of *Ceratolejeunea* tends to sug-



FIGS. 44-54. *C. guianensis* (N. & M.) Steph. FIG. 44. A spore from an immature capsule. FIGS. 45-46. Initial stages in cell division in the development of the sporeling. FIG. 47. An eight-celled thallus within the exospore similar to the condition found in the other species of the genus. FIGS. 48-49. Early stages in the development of the sporeling in which an apical cell with two cutting faces is formed at one end. FIGS. 50-52A. Variations in the development of the multicellular cylindrical thallus from one end of which the leafy plant develops. FIG. 53. A sporeling in which the thallus is one layer of cells thick except just below the leafy shoot. FIG. 54. A characteristic mature sporeling showing the slender cylindrical thallus and the shoot with well developed primary leaves. All magnifications, $\times 400$. Nos. 46, 47, 49, 50-53 are from one capsule. Drawn from E. G. Britton, Coker, and Rowland, 831, Trinidad.

gest that the species has been incorrectly assigned to this genus. The absence of well developed horns on the perianth might also be used as an argument in favor of this line of thought. On the other hand, the fact that in at least some of the capsules, sporelings occur which follow, in the earlier stages at

least, the plan of development observed in other species of the genus (an eight-celled thallus stage in the exospore in figure 47, and a secondary thallus with an apical cell with two cutting faces in figure 49), causes one to question such a conclusion. With only our present information there can be no decisive answer.

Of the 12 species discussed above, ten of them indicate a common basic pattern of sporeling development. The remaining species, *C. malleigera* and *C. guianensis*, in addition to a difference in the sporelings, also have other characters which to a greater or lesser degree are at variance with the characteristics of the genus *Ceratolejeunea*. Both species also have some vegetative characteristics which are definitely of the *Ceratolejeunea* category. Such species present a difficult and puzzling problem to the taxonomist, and the discovery of sporeling patterns different from that of the other species of the genus only adds to the difficulties involved.

Our knowledge of the sporelings, together with their patterns of development and range of variation, in the other genera of the family *Lejeuneaceae* is still too meagre to be of assistance in the interpretation of the puzzling problems presented within the genus *Ceratolejeunea*. The results to the present time indicate, however, that within limits these patterns do serve to show relationships and therefore can be of service in both taxonomic and phylogenetic interpretations.

2. VEGETATIVE REPRODUCTION

Vegetative reproduction has been mentioned in the genus by Evans⁶ (p. 277), who states that it is not unusual for a leaf cell to give rise directly to a leafy shoot or propagulum without the interpolation of a protonemal structure; and by Degenkolbe⁷ who quotes Evans (p. 59), and later lists *Ceratolejeunea* as having two records of brood bodies of the thallose form (p. 89). He does not describe or figure these structures.

Vegetative reproduction from ordinary leaf cells was seen in eight of the species studied. Except for *C. caducifolia* the phenomenon was of infrequent occurrence, and in many of the species only one or two examples have been observed, although a quantity of material has been examined. Except in *C. caducifolia* the leaves on which they occurred were attached to the stem.

The story of development of the new plants in all of the species except *C. caducifolia* is briefly as follows. An apparently mature cell of a leaf dedifferentiates and bulges, usually on the dorsal surface. Then, through the formation of a wall, in optical view at right angles to the long axis of the

⁶ Evans, A. W. Hepaticae of Puerto Rico. V. *Ceratolejeunea*. Bull. Torrey Club 32: 273-290. pl. 19, 20. 1905.

⁷ Degenkolbe, W. Brutorgane bei heblätterten Lebermoosen. Ann. Bryol. 10: 43-96. f. 1-112. 1937.

cell, two cells are formed. Further divisions in these bring about the formation of an apical cell with three cutting faces, which initiates the formation of the leafy plant. Rounded, undifferentiated cells are always present in greater or lesser numbers around the base of the stem. These cells were



FIG. 55. *C. spinosa* (G.) Steph. Ventral view of a young plant, $\times 90$, from Evans, Puerto Rico. FIG. 56. *C. flagelliformis* (Steph.) Fulford. Ventral view of a young plant, $\times 400$, from Brenes 19066, Costa Rica. FIGS. 57-61. *C. maritima* (Spr.) Steph. FIG. 57. Ventral view of a young plant, - X the underleaf, $\times 90$. FIG. 58. Dorsal view of the same plant, $\times 200$. FIG. 59. Detail of the base, $\times 400$. FIG. 60. Ventral view of a plant $\times 90$. FIG. 61. Detail of the base, $\times 400$. FIGURES 57-59 from Mosén 266, Brasil; figures 60-61 from Duss 634, Martinique.

formed through several divisions of the first pair of cells from the original leaf cell, but they did not become a part of the structure of the stem. *

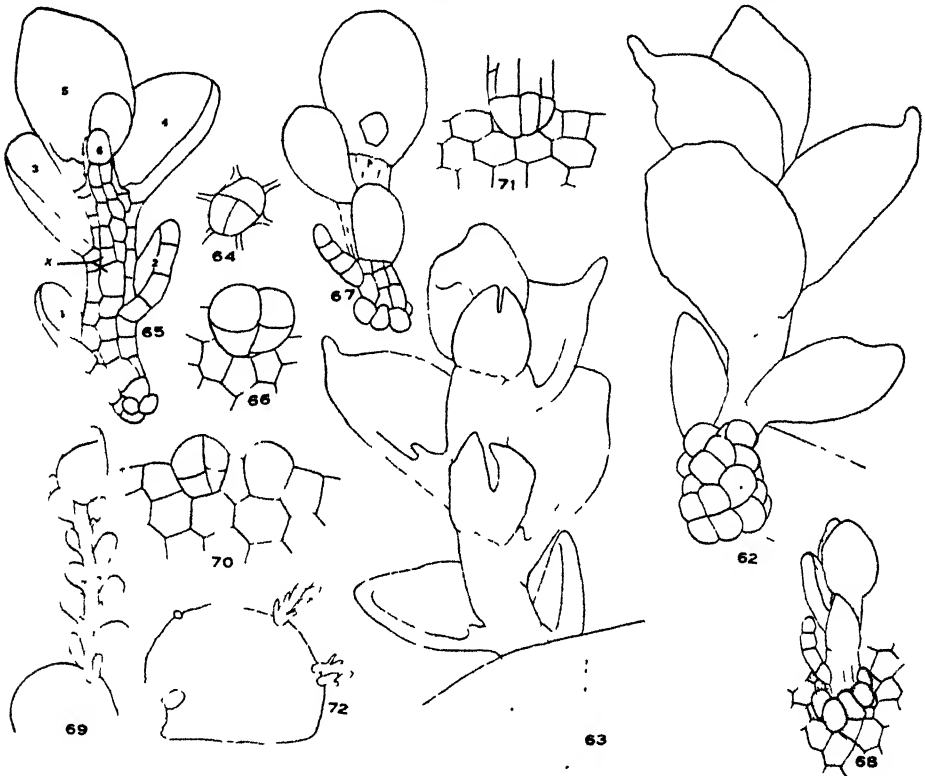
Leaves of the primary type usually precede the formation of the small leaves with ventral lobes. So long as only one row of ventral cells is formed from the ventral segment, no underleaves develop; but they make their appearance soon after two ventral rows are established. The first underleaf is in most plants undivided, but stems on which only the bifid type occur are occasionally met with. More detail of the development can best be brought out under the individual species.

C. SPINOSA (G.) Steph. (Figure 55.) The figure represents the only example of regeneration observed in this species. The shoot originated on the dorsal side of the leaf and had become very long. A number of rounded cells surround the base of the stem, and two rhizoids have been produced near the base. The first leaf suggests the primary leaf of the sporeling, but the other leaves suggest the pattern of the adult leaves rather than juvenile leaves, since the water-sac is less than half the size of the dorsal lobe. The first underleaf is elongate and undivided, but the rest are orbicular and bifid and more nearly approach the adult type.

C. FLAGELLIFORMIS (Steph.) Fulford. (Figure 56.) Several examples of regeneration were found in a collection of this species made by Brenes in Costa Rica. The species characteristically produces numerous flagelliform branches, some of them so slender and with leaves so greatly reduced that they suggest the shoots which have developed from leaf cells. The position of origin will at once distinguish the two. The larger leaves of the flagelliform branches are coarsely toothed, but the smaller ones are entire and similar to those of the stems from leaf cells. The plant seen in figure 56 developed on the dorsal surface of a leaf from a cell with thick walls, located half a dozen cells from the margin. From the ventral surface it could be seen that this cell had divided into two and that one of these new cells had divided again. Very few rounded cells were formed at the base of the stem. The first underleaf is undivided but the later ones are bifid. Some of the leaves were of the primary type, plane, others had water-sacs of one sort or another.

C. MARITIMA (Spr.) Steph. (Figures 57-61.) Figures 57-59 show the sort of plant produced in regeneration in that variant of the species in which the leaves are characterized by a "nerve" of large ocelli. Plants of this sort apparently regenerate more readily than those of the other variations of the species, for the new plants were present in many of the collections. They are always robust, with the basal rounded cells fairly numerous and conspicuous. The first leaves are of the primary sort (figs. 57, 58); they are followed by leaves with large water-sacs but which are less saccate than the juvenile

leaves. Three of these leaves show the row of ocelli. The first underleaf is undivided. Figures 60 and 61 illustrate a plant produced through regeneration in another of the variants of the species, one in which ocelli are solitary or in pairs and basal. This plant is very similar to that shown in figures 57 and 58 except that the first underleaf is bifid. The first underleaf of other



FIGS. 62, 63. *C. patentissima* (H. & G.) Evans. FIG. 62. Dorsal view of a young plant, $\times 200$. FIG. 63. Ventral view of the same plant, $\times 200$. From *Stehle 3638b*, Martinique. FIGS. 64, 65. *C. cornuta* (Lindenb.) Steph. FIG. 64. Mature leaf cell which has gone through two divisions on the way to the formation of a new plant, $\times 400$. FIG. 65. Ventral view of a young plant, $\times 200$. From *Fendler*, Trinidad. FIGS. 66, 67. *C. guianensis* (N. & M.) Steph. FIG. 66. An early stage in regeneration, $\times 400$, from *Small, Mosier and Small 6158* in Florida. FIG. 67. Dorsal view of a young stem, $\times 200$, from *Britton & Shafter 1724* in Puerto Rico. FIG. 68. *C. cubensis* (Mont.) Schiffn. Dorsal view of a young plant, $\times 200$, from *Evans 348*, Jamaica. FIGS. 69-72. *C. caducifolia* (Spr.) Steph. FIG. 69. Ventral view of a young plant, $\times 90$. FIG. 70. Portion of the margin of a leaf with two cells in early stages of regeneration, $\times 400$. FIG. 71. Detail of the base of a shoot on the margin of a leaf, $\times 400$. FIG. 72. A leaf with four marginal shoots, $\times 90$. From *Spruce, Manãos*, Brazil.

shoots on different leaves was undivided. Figure 61 shows that here, as in the other plants, a distinct group of rounded cells is developed at the base of the new shoot.

C. PATENTISSIMA (H. & G.) Evans. (Figures 62, 63.) Figures 62 and 63 show both the dorsal and ventral views of the only example which was seen. The rounded basal cells are numerous. Most of the leaves are pointed, a character not observed in the young plants of the other species. All the leaves show some development of a ventral lobe. All the underleaves are definitely bifid.

C. CORNUTA (Lindenb.) Steph. (Figures 64–65.) Figure 64 shows an early stage in the development of a new shoot from a leaf cell. The enlarging leaf cell has bulged on the dorsal surface and divided twice. Figure 65 shows a young plant in which only a few of the rounded, basal cells were developed. Three of the leaves, nos. 1–3, are of the primary type and nos. 4 and 5, which follow, give an indication of the development of the ventral lobe. It is of interest to note that up to the point of the formation of the third leaf, only one row of ventral cells has developed (see x in fig. 65), but at this point two rows can be observed. It is after these two longitudinal rows have become established that an underleaf, no. 6, makes its appearance. It is undivided.

C. GUIANENSIS (N. & M.) Steph. (Figures 66 and 67.) Figure 66 shows an early stage (but somewhat later than that of figure 64), in the development of the new shoot. Figure 67 shows a leafy plant. The leaf at the top of the stem has a single large ocellus. Few rounded cells were developed at the base of the stem. Other larger plants in which there were half a dozen pairs of leaves of the primary and juvenile types were occasionally seen. These were similar to the shoots of *C. maritima* except that very few rounded cells were formed at the base.

C. CUBENSIS (Mont.) Schiffn. (Figure 68.) Regeneration is not uncommon in plants of this species. Most of the shoots were small, and had produced only a few leaves, of the primary type. Rounded cells are conspicuous at the bases of the shoots. Figure 68 is representative. It suggests the shoots of *C. cornuta* and *C. guianensis* shown in figures 65 and 67.

C. CADUCIFOLIA (Spr.) Steph. (Figures 69–72.) Regeneration in this species is somewhat different from that in those just described, since the new plants usually arise from the marginal cells of the leaves. A cell bulges beyond the normally crenulate margin (see figure 70). Next a wall at right angles to the margin and to the plane of the leaf divides the cell into two (fig. 70). Most of these cells again divide at right angles to the first wall and to the plane of the leaf (fig. 70). The next divisions initiate the formation of an apical cell with three cutting faces. Through the activities of this cell the leafy plant is developed. Every cell formed through the early divisions of the marginal cells becomes a part of the stem, and there are no rounded, undifferentiated cells at the base of the stem as there are in the other species.

The leaves of the new plant all give some indication of a ventral lobe (fig. 69). In some of the stems which were examined there is only one row of cortical cells developed from the ventral segment, and underleaves are absent. Some of the new shoots were very long and some of these developed juvenile leaves for a time, so that a stem often shows a variety of leaves (see figure 69). No underleaves were observed.

In all these species the pattern of development of a new shoot from a leaf cell through regeneration is more or less uniform. The development in *C. caducifolia* is somewhat different, but only in that the new shoots usually arise from cells of the margin rather than from the interior of the leaf. This same pattern of regeneration also occurs in *Frullania Asagrayana*, *Leucolejeunea clypeata*, etc., and thus appears to be of little significance as an aid in the taxonomy of the genus or the species.

SUMMARY

1. Sporelings

1. Sporelings of twelve species of *Ceratolejeunea* have been studied.
2. The sculpturing of the spore coat was similar in all of the species, and like that of several of the other genera of the *Lejeuneaceae*. The exospore is papillose with additional thickenings in the form of scattered "rosettes."
3. The sporelings show a fundamental basic pattern of development which may well be designated the *Ceratolejeunea* type. In this, a thallus two cells broad and four cells long is formed within the exospore. An apical cell with two cutting faces develops from one of the cells at the end, and the segments cut off from it form the secondary thallus which becomes four cells broad and of indefinite and variable length. Eventually, the apical cell of this thallus becomes transformed into an apical cell with three cutting faces and the leafy axis is formed through its activities. In *C. malleigera* and *C. guianensis* exceptions to this pattern occur.
4. There is some variation among the sporelings of a single species:
 - a. Variations of the thallus within the exospore take the form of fewer cells; or of more cells, which are formed through the division of one or more of the original eight cells; or of a second apical cell at the opposite end.
 - b. Variations of the secondary thallus have to do primarily with its length and less often with its width. Often it is only one or two cells long when the leafy plant is formed. Branching from marginal cells is not uncommon.
5. The leafy stem develops at the growing tip of the secondary thallus. The first leaves are of the primary type and are followed by the leaves with large water-sacs, the juvenile leaves.
6. The pattern of development of the sporelings appears to be constant within the genus (when *C. malleigera* and *C. guianensis* are excepted), and

may be used to advantage in the taxonomic study of species whose position has been regarded as doubtful.

7. *C. malleigera* may be considered an aberrant species, for only two horns are developed on the perianth and the secondary protonema of the sporeling is six cells broad instead of four.

8. *C. guianensis* exhibits a mature sporeling of entirely different pattern from that of the other species studied. It is long, slender, and cylindrical. Whether this difference should be regarded as significant in relation to the taxonomic position of the species cannot be demonstrated at the present time.

9. There is every indication from this study that sporeling patterns can be of assistance in generic determinations; and that a knowledge of these patterns will aid materially in the reconstruction of phylogenetic relationships.

2. Vegetative Reproduction

10. The single leaf cell which gives rise to the new plant is totipotent.

11. The cell bulges (usually on the dorsal surface of the leaf), and after several divisions an apical cell with three cutting faces is formed. In most species some of the early cells formed divide several times more and remain as a collar of rounded, unspecialized cells at the base of the stem.

12. The first two leaves formed are usually of the primary type, and those which follow are usually of a modified adult form. Juvenile leaves occur only occasionally.

13. Usually only one vertical row of cortical cells from the ventral segment occurs on the lower part of the stem. It is only after two rows become established that the underleaves are formed.

14. The first underleaf of most new plants is undivided, the later ones are bifid.

15. The pattern of development of the new shoots of *C. caducifolia* differs from that of the other species in that each arises from a marginal cell, and no supplementary rounded cells are formed at the base of the stem.

I wish to express my appreciation to Dr. A. W. Evans who has given generously of his time in reading the manuscript and in making suggestions and criticisms; to Dr. H. W. Rickett for helpful suggestions; and to the New York Botanical Garden for the use of the Library and the Herbarium and for facilities for work.

UNIVERSITY OF CINCINNATI

AND

THE NEW YORK BOTANICAL GARDEN

A NEW PARASITIC RED ALGA FROM SOUTHERN CALIFORNIA

ELMER YALE DAWSON

Kylin¹ recognizes three parasitic genera in his monograph of the Delesseriaceae: *Gonimocolax*, *Polycoryne*, and *Gonimophyllum*, all of which are arranged as members of the Nitophylleae. *Gonimophyllum* is placed in the Cryptopleura Group because the gonimoblasts bear terminal carpospores, while the other two genera are placed in the Myriogramme Group in which the gonimoblasts bear carpospores characteristically in chains. All three genera lack growth from an apical cell, except in young stages, and intercalary division of the primary cell row is typical.

A new and very distinctive parasitic genus, *Loranthophycus*, is described below, distinguished from the other parasitic Delesseriaceae by its mode of growth from an apical cell, and by the absence of intercalary division of the primary cell row. The divisions of the apical cell are not limited to young stages, but continue through the entire growth of the thallus. Although this is not yet confirmed by studies of cystocarpic plants, from the evidence at hand *Loranthophycus* seems to be a degenerate member of the Membranoptera Group of the Delesseriaceae in which (1) growth is from an apical cell, (2) tertiary cell-row initials do not reach the thallus margin, and (3) intercalary division of the primary cell row is absent.

Loranthophycus Dawson, gen. nov.

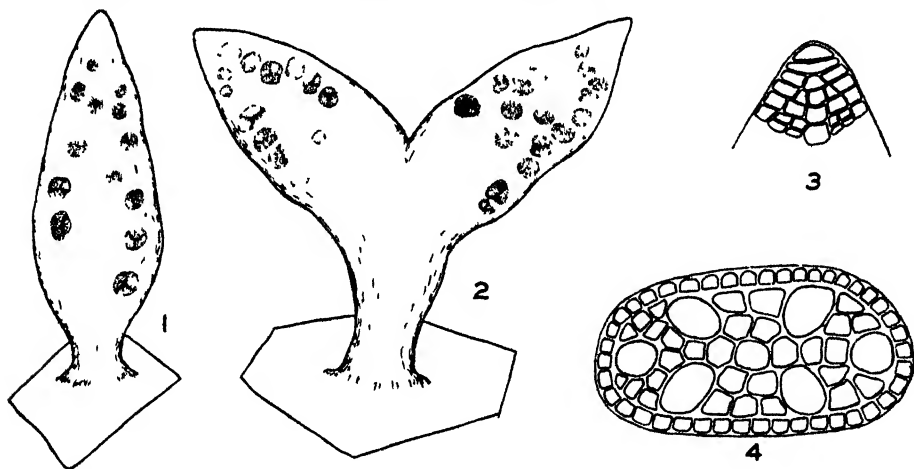
Thallus minutulus, parasiticus, dilute roseus; partibus fertilibus e pulvino humili in hospite, lanceolatis, compressis, brevistipitatis, cellula apicali sine divisionibus cellularum intercalarium in primario ordine crescentibus; cellula prima tertii ordinis non in margine posita; tetrasporangiis tripartitis, per totam frondem sparsis; cystocarpiis antheridiisque nondum visis.

Plants minute, parasitic; fertile thalli pale rose-colored, arising from a very low, inconspicuous, cushion-like point of union with the host, lanceolate, compressed, with a short stipe; growth from an apical cell which cuts off a thin, saucer-shaped cell basally, this soon divided by two inclined lateral walls to set off the initials of the primary (central) and secondary cell-rows; secondary cell-row initial remaining at frond margin; tertiary cell-row initials not reaching margin; lateral divisions to form pericentral cells beginning very near the apex; intercalary division of primary cell row absent; tetrasporangia tripartite, borne abundantly throughout the expanded part of the fertile thallus beneath the small-celled surface layer; cystocarps and antheridia unknown.

¹ Kylin, H. 1924. Studien über die Delesseriaceen. Lunds Univ. Årsskr. 11, Afd. 2, 20: 1-111.

Loranthophycus californicus Dawson, sp. nov. (Figs. 1-4.) Frons brevistipitate, plerumque sola e strato basilari pulvinato, circiter 1 mm. alta; laminis lanceolatis compressis, integris, simplicibus aut bifurecatis, circiter 400 μ latis, 200 μ crassis; tetrasporangiis per totam frondem sparsis, maturi 90-100 μ diam.; cystocarpis antheridiisque nondum visis.

Fertile fronds usually arising singly from the basal cushion, about 1 mm. long, lanceolate, compressed, acute above, narrowed below to a short, thick stipe; blades entire, simple or commonly forked, sometimes 3-lobed, the segments about 400 μ broad, 200 μ thick, of several layers of cells; surface cells 16-20 μ broad in surface view, forming an even epidermal layer; medullary cells 25-35 μ in greatest diameter; tetrasporangia scattered throughout the expanded frond in the outer medulla beneath the epidermis; mature quartets of tetraspores 90-100 μ in diameter; cystocarps and antheridia unknown.



FIGS. 1-4. *Loranthophycus californicus* Dawson. FIG. 1. A mature, simple tetrasporic plant. $\times 50$. FIG. 2. A mature, forked tetrasporic plant. $\times 50$. FIG. 3. Median optical view of the growing apex showing apical cell. $\times 350$. FIG. 4. Cross section of mature tetrasporic frond showing tetrasporangial cavities. $\times 100$.

TYPE: Parasitic on sterile fronds of an undescribed delesseriaceous plant dredged from rocky bottom at a depth of 25 meters off Point Loma, San Diego County, California, March 10, 1944. Deposited in the Herbarium of the University of California.

Loranthophycus californicus has been noted in but a single collection in which tetrasporic plants alone occurred in great abundance. A study of cystocarpic plants, therefore, may be expected to demonstrate more precisely the relationships of this peculiar plant.

Since most parasitic algae are limited to a single host and usually belong to the same family as does the host, the present inability to give specific identity to the plant upon which *Loranthophycus californicus* grows is not entirely satisfactory. It seems clearly delesseriaceous in structure, however, and vegetatively fits very nicely in the austral genus *Platyclinia* alongside

of *P. Crozieri*. The plant may, indeed, prove to be an undescribed boreal genus closely related to *Platyclinia*. For purposes of identification the following brief characterization is given.

Fronds erect, to 12 cm. high, membranous, rose-colored, attached firmly to rocks by means of a thin, adherent crust augmented by a few, short, clasping stolons, expanded from a branched, subterete stipe 1.0–1.5 cm. high; blades 3–4 from each main stipe, narrowly cuneate for 1.5–2.0 cm. above the point of branching, then expanding abruptly into a thin, smooth, veinless, narrow ovate, membranous portion 3–4 cm. broad, this usually simple, but sometimes dividing above the middle into two broad lobes; margins irregularly shallowly lobed or simply undulate; membranous parts with an external layer of small, flattened, pigmented, squarish cells and several irregular, medullary layers of large, colorless, thin-walled cells.

Acknowledgment is due to Dr. Martin W. Johnson who collected the type specimens.

SCRIPPS INSTITUTION

LA JOLLA, CALIFORNIA

A NEW *MONARDA* (LABIATAE) AND A NEW *CALOCARPUM* (SAPOTACEAE) FROM MEXICO

CHARLES LOUIS GILLY

From collections made in various parts of Mexico during the year 1943, by members of a group on leave of absence from or associated with the New York Botanical Garden, the two entities below are selected as being worthy of description.

Monarda malloryi Gilly, sp. nov. Herba perennis; caule simplici vel ramoso; foliis serratis, supra glabris, subtus strigilloso-hirsutis ad venas, e deltoideo-lanceolatis ad deltoideo-ovata; foliorum laminis maximis 5.5-7.0 cm. longis, 2.4-3.0 cm. latis; calycibus 8-12 mm. longis, glabris, in ore dense hirsutis; corolla rubra vel rubro-magenta, 23-34 mm. longa, ore 3-4 mm. lato; staminibus sub ore corollae 3-4 mm. insertis.

Perennial herbs to at least 1.2 m. tall; stems simple or branched, glabrous to sparsely hirsute particularly on the angles and at the nodes. Leaves deltoid-lanceolate to deltoid-ovate, serrate (the teeth 3-6 mm. apart), glabrous on the upper surface, glabrous beneath except for sparse strigillose-hirsute pubescence on the veins, the largest 5.5-7.0 cm. long and 2.4-3.0 cm. wide, broadest 6-10 mm. above the base, scarcely more than one-half as long as the internodes which they subtend; median petioles 5-10 mm. long. Glomerules of the inflorescence solitary at the apices of the main stem and branches (when these are present), 1.5-3.0 cm. in diameter excluding the corollas; subtending bracts foliaceous, red-tinged or completely red on the upper surface, pale green beneath, glabrous above and below except for the strigillose-hirsute veins below, deltoid-lanceolate to lanceolate-elliptic, sub-petiolate, the larger 2.5-4.0 cm. long and 1.2-2.8 cm. wide. Calyces 8-12 mm. long, glabrous externally, the orifice densely hirsute; calyx-teeth 1-1.5 mm. long, glabrous or minutely pubescent but not glandular. Corollas crimson to crimson-magenta, sparsely pubescent with crisp hairs, 2.3-3.4 cm. long, 3-4 mm. broad at the throat, the constricted portion of the tube 8-14 mm. long. Stamens attached 3-4 mm. within corolla throat, exceeding the galea by 3-6 mm.; filaments glabrous, 12-15 mm. long; anthers 3 mm. in length. Style glabrous, exserted 3-8 mm. beyond the galea.

TYPE: MEXICO—Veracruz: near Piletas, July 14, 1943, *Donald Dodds 105* (NY). Probably also referable here are *Purpus 6048*, *Plunkett s. n.*, and *Leibmann 15583*, from the same general area, which have been doubtfully referred to *M. Pringlei* Fernald by McClintock and Epling (Univ. Calif. Publ. Bot. 20(2): 161. 1942).

The species is named in honor of Dr. Lester Dewitt Mallory, Agricultural Attaché of the U. S. Embassy in Mexico City, whose co-operative interest has been of utmost value in furthering recent collecting in Mexico. Although most closely allied to *Monarda pringlei* Fernald of Nuevo León and Coahuila, and exhibiting certain tendencies toward *M. bartlettii* Standley of Tamaulipas, this entity—which should be an interesting garden subject wherever it can be grown—definitely merits specific recognition.

Calocarpum huastecanum Gilly, sp. nov. Arbor lacticifera; foliis subcoriaceis, supra atroviridibus subtus pallido-viridibus, glabris praeter petiolos et venulos subtus permanentiter brunneo-tomentosos; laminis oblanceolatis vel anguste obovatis; floribus pedunculatis, fasciculatis vel solitariis; bracteis floriferis lanceolatis ad lato-orbicularibus; perianthio luteo-albo, lobis quadrato-ellipticis; antheris et perianthii lobis subaequalibus; staminodiis staminodiorum filamentis consimilibus; ovario in anthesi conico pubescenti; fructu ignoto.

Tree with soft wood and milky sap to at least 30 m. in height and with stem to 1 m. in diameter. Leaves clustered at the apices of branches, subcoriaceous, dark glossy green above, pale green beneath, glabrous except for the petiole and the veins beneath which are densely and persistently brown-tomentose; leaf-blades oblanceolate to narrowly obovate, acuminate at the apex, 20-35 cm. long and 4-7 cm. wide; petioles stout, terete, 2-5 cm. long. Flowers solitary in axils of leaves of the season and grouped in small clusters above the old leaf-scars, shortly pedunculate, the stout peduncles 1-3 mm. in length. Floral bracts (which simulate an imbricated calyx) 5-8, minutely tomentose, yellowish-green with brown margins, entire, emarginate or crose at the apices, the outermost minute and lanceolate, the innermost broadly orbicular and to 4.5 mm. long and 5 mm. wide. Perianth subfleshy, 5-lobed, pale yellowish-white, 6-9 mm. in length and to 10 mm. in diameter at anthesis, the lobes spreading, quadrate-elliptic, rounded to almost truncate at the apices, 3-4.5 mm. long and 2.5-3.5 mm. wide. Stamens 5, attached at the summit of the perianth-tube opposite the lobes, equaling or slightly exceeding them in length; anthers narrowly sagittate, 1-1.5 mm. long. Staminodes subfleshy, terete, acute, 1-2.5 mm. long, resembling the filaments of the stamens and attached between the lobes of the perianth. Ovary at anthesis 2-3 mm. in diameter, conical, multi-ribbed, short-pubescent; style glabrous or sparsely minutely pubescent, apically truncate, 3-5 mm. long. Fruit not definitely known; said by natives of the area to be ovoid-globose, blunt at the apex and about 12-15 cm. long.

TYPE: MEXICO--San Luis Potosí; north of Tamazunchale at Km. 387 on the Laredo-Mexico City highway, July 14, 1943, *C. L. Gilly and H. W. Rickett* 12 (NY).

The specific name is based on the common native geographical designation of the area towards the western margin of which the type was collected. The species differs from the other known species of the genus in Central America and Mexico principally by the persistent ferrugineous pubescence of the leaves, by details of the flower structure and, possibly, in the size and shape of the fruit.

NOTE: Since this paper was submitted for publication I have received a communication from Dr. C. L. Lundell, of Southern Methodist University, who observed the tree—from which the type was obtained—on November 6, 1943. He writes: "The small ovoid fruits were scarcely more than two inches long." Whether the fruits had at that time attained their mature size is not definitely known.

MEXICO, D. F.

THE FERNS OF GILGIT, BALTISTAN, AND LADAK

RALPH R. STEWART

Most of the region covered by this paper is north of the Indus River and comprises the northernmost part of the British Indian Empire. It is north of the main Himalayan chain; the chief mountains are the Karakorums. Renato Pampanini (1930) in *La Flora del Caracorum* lists only five ferns and two species of *Equisetum*. I have visited parts of this region, and have obtained records of 25 additional ferns from this little known part of Central Asia.

The Karakorum Mountains form a massive barrier with passes 18,000 feet or more in height, shutting off practically all intercourse between Kashmir and the territory to the north. In this region are the largest glaciers outside of the arctic and here is to be found Mt. Godwin Austen, the second highest mountain in the world.

Gilgit, or more correctly, the Gilgit Agency, is just west of Baltistan and outside of Kashmir proper. The Gilgit Cantonment is a little less than 5000 feet in altitude and much lower than the rest of the area, which is very high and extremely rugged.

Ladak and Baltistan are the two chief divisions of the country to the north of the main range of the Himalayas in Kashmir State. They are both drained by the Indus and its tributaries. In the *Flora of British India* (Hooker 1872-1896) this region is called Western Tibet. Baltistan used to be called Little Tibet. In this paper the Deosai region south of Skardu is included in Baltistan, and Dras as part of Ladak.

The Indus at Skardu, the chief village in Baltistan, is about 7600 feet above sea level, while at Leh, the capital of Ladak, it flows at 11,000 feet. The whole country is mountainous. There is very little rain; the average at Leh is 2.7 inches a year. There is, however, much snow, which falls in the winter on the high mountains. There is little rain or snow in the main valleys. It is not a good country for ferns and none of the ferns in this list is abundant except *Cystopteris fragilis*. There are no real forests but in favorable places juniper forms trunks of good size without attaining much height.

Little work has been done on the ferns of Kashmir and the territory to the west. In the *Journal of Botany* for 1896 C. W. Hope published a list of 27 ferns which had been gathered by Gen. W. Gatacre on the Chitral Relief Expedition. Chitral is on the Afghan frontier southwest of Gilgit. His report includes a few ferns from lower levels. Most of the ferns here recorded grow at altitudes of from 8000 to 12000 feet, while a few grow even higher. They are chiefly temperate or alpine forms, except for *Ceterach officinarum* and

Cheilanthes persica, which are Mediterranean ferns growing at the eastern extremity of their range in the hot, dry, Indus valley.

The most useful work for those interested in the ferns of North India is C. W. Hope's "Ferns of Northwestern India," published in parts in the *Journal of the Bombay Natural History Society* from 1899 to 1904. Many of the records which follow are to be found in this work.

In spite of the inaccessibility of the region it has been visited by a good many explorers, beginning with William Moorcroft in 1820. Pampanini (1930) gives an excellent list of the visitors who collected plants, together with a bibliography and an account of the routes followed. The only omission I notice is the failure to mention the name of J. E. Winterbottom in connection with the Tibetan Boundary Delimitation Commission of 1847-1848.

Most of the specimens mentioned are in the Dehra Dun Herbarium of the Imperial Forestry Research Institute in North India and in the Royal Botanic Gardens at Kew. Many of them are in the Gordon College Herbarium at Rawalpindi in North Punjab.

I have omitted *Equisetum diffusum*, which I reported from Ladak in 1917, for I now consider it to be *E. arvense*. According to Pampanini, Wallich had a specimen of *Pteris longifolia* (*vittata*), which Moorcroft gathered in Ladak. I suspect an error, for no one else seems to have found it above 6500 feet. It grows farther down the Indus near Mt. Nanga Parbat in the hot zone.

OPHIOGLOSSACEAE

BOTRYCHIUM LUNARIA (L.) Sw. Karakorum Mts., *Clarke*; W. Tibet, *Falconer*.

POLYPODIACEAE

CYSTOPTERIS FRAGILIS (L.) Bernh. The only fern common throughout, from 7000 to 14000 feet.

DRYOPTERIS BLANFORDII (Hope) C. Chr. Baltistan, 12000-13000 feet, *Duthie*. Cited by Hope.

DRYOPTERIS ODONTOLOMA (Moore) C. Chr. Gilgit, in 1847, 10000 feet, *Winterbottom*. Cited by Hope.

DRYOPTERIS RAMOSA (Hope) C. Chr. Dras Valley, 10000 feet, *Duthie* 11677.

DRYOPTERIS BARBIGERA (Moore) Kuntze. Mitsahoi, Ladak Road, 11000 feet, *Stewart* 13151.

DRYOPTERIS BRUNONIANA (Wall.) O. Kuntze. Ascent Mir Panzil Pass to the Deosai Plains, 12000 feet, *Stewart* 19991.

DRYOPTERIS LINNAEANA C. Chr. Gilgit, *Winterbottom*; near Parkutta, Indus Valley, Baltistan, 8000 feet, *Stewart* 20915.

DRYOPTERIS LEVINGEI (Clarke) C. Chr. Gilgit, Herb. Dehra Dun.

POLYSTICHUM LONCHITIS (L.) Roth. Gilgit, *Duthie*. Cited by Hope.

POLYSTICHUM LACHENENSE (Hk.) Bedd. Gor. Gilgit, 15000 feet, *Tanner*.

POLYSTICHUM PRESCOTTIANUM (Wall.) Moore. Sai, Gilgit, *Tanner*; Parkutta to Tolti, 8000 feet, Baltistan, *Stewart* 20928; Chunnagund, Ladak, 9000 feet, *Stewart* 21053.

POLYSTICHUM THOMSONI (Hook.) Bedd. Tarkiti, 8000 feet, Indus Valley and Shyok Valley, Baltistan, *Thomson*; Mir Panzil Pass, 12000 feet, *Stewart 20005*.

ATHYRIUM FILIX-FEMINA (L.) Roth. Ascent Mir Panzil Pass, 12000 feet, *Stewart 19945a*. Approaches var. *retusa* Clarke.

ATHYRIUM RUPICOLA (Hope) C. Chr. Near Bagicha, Indus Valley, 8500 feet, near waterfall, *Stewart 20980* (Det. Morton).

ASPLENIUM VIRIDE Huds. Gilgit, *Tanner, Giles*; Mitsahoi, Ladak Road, 11000 feet, *Stewart*.

ASPLENIUM TRICHOMANES L. Gilgit, 5500 feet, *Tanner*; Satpura Nullah, Baltistan, 10000–11000 feet, *Duthie*. Herb. Dehra Dun.

ASPLENIUM SEPTENTRIONALE (L.) Hoffm. Gilgit, Herb. Dehra Dun.

ASPLENIUM RUTA-MURARIA L. Shingo Valley, Baltistan, 10000–11000 feet, *Duthie*; Kangi Nullah, Ladak, 13500 feet, *Koelz 2828*.

ASPLENIUM FONTANUM (L.) Bernh. Gilgit, *Tanner, Giles*; Baltistan, 10000–11000 feet, *Duthie*; 7600 feet, *Winterbottom*.

ASPLENIUM VARIANS Hook. & Grev. Near Skardu, Baltistan, *Thomson*; near Bagicha, Indus Valley, Baltistan, 8500 feet, *Stewart 21002*.

CRYPTOGRAMMA BRUNONIANA Wall. Ascent Mir Panzil Pass to Deosai, 13000 feet, *Stewart 19986*.

CRYPTOGRAMMA STELLERI (Gmel.) Prantl. Karakorum Mts., 12500 feet, *Clarke*; Chunagund, Ladak, 9500 feet, *Stewart 21059*.

CETERACH OFFICINARUM DC. Gilgit, 8000 feet, *Tanner*, Herb. Dehra Dun.

CHEILANTHES PERSICA (Bory) Mett. Gilgit, 7000 feet, *Tanner*; Skardu, Baltistan, 8000 feet, *Stewart 20128*; Above Kuru, Shyok Valley, *Stewart 20860* and *Kiris 20891*.

CHEILANTHES DALHOUSIAE Hook. Near Bagicha, Baltistan, 8500 feet, *Stewart 20961, 21003*.

ADIANTUM CAPILLUS-VENERIS L. Kangi Nullah, Ladak, 12500 feet, *Koelz 2821*; Kuru to Kiris, Shyok Valley, 8000 feet, *Stewart*.

PTERIDIUM AQUILINUM (L.) Kuhn. Gilgit, *Giles*. Herb. Dehra Dun.

POLYPODIUM CLATHRATUM Clarke. *Duthie*, Herb. Dehra Dun.

EQUISETACEAE

EQUISETUM ARVENSE L. Khalotse to Lamayuru, Ladak, 9500 feet, *Stewart 138a*; Shimsa Kharbu, Ladak, *De Terra* and *Hutchinson*, Herb. New York; Dras Valley, *Osmaston*, Herb. Dehra Dun.

EQUISETUM RAMOSISSIMUM Desf. Common in Baltistan and Ladak.

LYCOPODIACEAE

LYCOPODIUM SELAGO L. Gilgit, 12000 feet; Burzil Pass, near Deosai, *Koelz 9410*.

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